IMPERIAL INSTITUTE
OF
AGRICULTURAL RESEARCH, PUSA.

PROCEEDINGS

OF THE

GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

OF THE

ZOOLOGICAL SOCIETY

OF LONDON.

1928, pp. 1–660,

WITH 34 PLATES AND 208 TEXT-FIGURES,
AND INDEX TO PAGES 1–660.

PRINTED FOR THE SOCIETY,
SOLD AT ITS HOUSE IN REGENT'S PARK.
LONDON:
MESSRS. LONGMANS, GREEN, AND CO.,
PATERNOSTER ROW

LIST
OF THE
COUNCIL AND OFFICERS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.
1928–1929.

Patron.
His Majesty The King.

COUNCIL.

His Grace The Duke of Bedford, K.G., F.R.S., *President.*

Sir John Bland-Sutton, Bt., F.R.C.S.

Charles Drummond, Esq., *Treasurer.*

Alfred Ezra, Esq., O.B.E.

The Rt. Hon. The Viscount Grey, K.G., P.C., F.R.S., *Vice-President.*

Prof. James P. Hill, D.Sc., F.R.S., *Vice-President.*

Major Stanley S. Flower, O.B.E., F.L.S., *Vice-President.*

Lt.-Col. The Lord Alastair Innes-Ker, D.S.O.

Sir Walter R. Lawrence, Bt., G.C.I.E., G.C.V.O.

J. Spedan Lewis, Esq.

Professor Ernest William MacBride, M.A., D.Sc., F.R.S., *Vice-President.*

Col. Sir A. Henry McMahon, G.C.V.O., G.C.M.G., K.C.I.E., C.S.I.

Henry G. Maurice, Esq., C.B.

Edmund G. B. Meade-Waldo, Esq.

P. Chalmers Mitchell, Esq., C.B.E., M.A., D.Sc., LL.D., F.R.S., *Secretary.*

The Rt. Hon. The Earl of Onslow, P.C., O.B.E., *Vice-President.*

Major Albert Pam, O.B.E.

Lt.-Col. Sir David Prain, C.M.G., C.I.E., F.R.S.

Richard S. Taylor, Esq.

Anthony Henry Wingfield, Esq., D.L.

Sir Arthur Smith Woodward, LL.D., F.R.S., *Vice-President.*

PRINCIPAL OFFICERS.

P. Chalmers Mitchell, C.B.E., M.A., D.Sc., LL.D., F.R.S., *Secretary.*

G. M. Vevers, M.R.C.S., L.R.C.P., *Superintendent of the Gardens.*

D. Seth-Smith, *Resident Curator of Mammals and Birds.*

Edward G. Boulenger, *Director of the Aquarium.*

Miss Joan B. Procter, F.L.S., *Curator of Reptiles.*

L. C. Bushby, F.E.S., *Curator of Insects.*

S. Zuckerman, M.A., *Anatomist.*

H. H. Scott, M.D., F.R.C.P., D.P.H., *Pathologist.*

Prof. G. H. Wooldridge, F.R.C.V.S., *Hon. Consulting Veterinary Surgeon.*

R. W. A. Salmond, O.B.E., M.D., *Hon. Consulting Radiologist.*

F. Martin Duncan, F.R.M.S., F.R.P.S., *Librarian.*

F. W. Bond, *Accountant.*

W. C. Harris, *Chief Clerk.*

LIST OF CONTENTS.

1928, pp. 1–660.

EXHIBITIONS AND NOTICES.

Page

The SECRETARY. Report on the Additions to the Society's Menagerie during the months of October, November, December, 1927, and January, 1928 265

Mr. D. SETH-SMITH, F.Z.S. Exhibition of a blue variety of Masked Lovebird (*Agapornis personata*) 266

Major S. S. FLOWER, O.B.E., F.Z.S. Exhibition of Photographs taken by Mr. G. C. Flower in the Red Sea ... 267

Dr. G. M. VEVERS, F.Z.S., and Mr. L. C. BUSHBY, F.E.S. Exhibition of specimens of the Mitten Crab (*Eriocheir japonicum*).. 267

The Hon. IVOR MONTAGU, F.Z.S. Exhibition of Photographs of the Moscow Zoological Gardens 267

Mr. G. C. ROBSON. Exhibition of lantern-slides illustrating some observations on the oviposition of *Octopus* 267

Mr. C. W. CHORLEY, F.Z.S. Notes on Uganda Gorillas ... 267

Mr. F. MARTIN DUNCAN, F.Z.S. Exhibition of Cinematograph Films taken in the Society's Gardens...... 268

The SECRETARY. Report on the Additions to the Society's Menagerie during the month of February, 1928 653

The SECRETARY. Exhibition of Photographs of the Detroit Zoological Gardens 653

Miss E. M. BROWN. Exhibition of Fluke (*Microcotype* sp.) from the Gills of a Sea Bream (*Pagellus centrodontus*). 653

Mr. F. MARTIN DUNCAN, F.Z.S. Exhibition of Trapdoor Spiders' Nests from Queensland, and a female Huntsman Spider (*Heterapoda venatorius*) with her egg-cocoon 653

Page

Mr. D. Seth-Smith, F.Z.S. Exhibition of a lead-pipe gnawed by Mice, and Photographs of the Society's New Bird House 653

Mr. E. G. Boulenger, F.Z.S. Exhibition of living specimens of *Pipa americana* 653

Major S. S. Flower, O.B.E., F.Z.S. Exhibition of living specimen of the Great African Tortoise *Testudo sulcata*. (Text-figures 1, 2) 654

Capt. C. R. S. Pitman, D.S.O., M.C. Note on Nkosi Island and its Sitatunga (*Tragelaphus spekii*) 655

Mr. C. F. M. Swinnerton, C.M.Z.S. Exhibition of Photographs showing forest undergrowth cleared by Sitatunga 657

Mr. D. Seth-Smith, F.Z.S. Exhibition of Photographs of a Pangolin 657

The Secretary. Report on the Additions to the Society's Menagerie during the month of March, 1928 658

Mr. Clarence Elliott. Exhibition of Giant Barnacles from Chile, and of a living specimen of the Giant Tortoise *Testudo microphyes* from Albemarle Island (Galapagos Islands) 658

Lord Rothschild, D.Sc., F.R.S., F.Z.S. Exhibition of Photographs and Skulls of Gigantic Land Tortoises . 658

PAPERS.

1. Age-Changes in the Chimpanzee, with special reference to Growth of Brain, Eruption of Teeth, and Estimation of Age: with a Note on the Taungs Ape. By S. Zuckerman, M.A. (Plates I.–IV.; Text-figures 1–3.) 1

2. Carcinoma of the Tonsil in a Common Wolf (*Canis lupus*). By H. Harold Scott, M.D., F.R.C.P., F.R.S.E., F.Z.S. (Plates I.–III.) 43

Page

3. On some Points in the Structure of Palæoniscid and allied Fish. By D. M. S. WATSON, F.R.S., F.Z.S. (Text-figures 1–15.) 49

4. Notes on East African Birds (chiefly Nesting-habits and Stomach-contents) collected in 1926. By ARTHUR LOVERIDGE, C.M.Z.S. 71

5. Report on the Deaths occurring in the Society's Gardens during 1927. By H. HAROLD SCOTT, M.D., F.R.C.P., F.Z.S. 81

6. Notes on some East African Invertebrates collected in 1926. By ARTHUR LOVERIDGE, C.M.Z.S. 121

7. Notes on Oriental Dragonflies [Odonata], with Descriptions of New Species. By the late Mr. H. CAMPION and by F. F. LAIDLAW, F.Z.S. (Text-figures 1–3.) ... 129

8. The Delacour Exploration of French Indo-China—Mammals. II. On Mammals collected during the Winter of 1926–27. By OLDFIELD THOMAS, F.R.S., F.Z.S. 139

9. New Chrysomelid Beetles from India. With a Note on the Scales of Coleoptera. By S. MAULIK, F.Z.S. (Text-figures 1–5.) 151

10. On a Collection of Land and Freshwater Mollusca from Southern Abyssinia. By M. CONNOLLY. (Plate I.; Text-figures 1–4.) 163

11. Studies and Observations bearing on the Phylogeny of the Ostrich and its Allies. By PERCY ROYCROFT LOWE, B.A., M.B., F.Z.S. (Plate I.; Text-figures 1–23.) 185

12. Tuberculosis in Marsupials. By H. HAROLD SCOTT, M.D., F.R.C.P., F.Z.S. (Plates I.–III.) 249

13. On the Giant Octopus of New Zealand. By G. S. ROBSON, M.A., F.Z.S. (Text-figures 1–6.) 257

14. The External Morphology and Life-history of the Coccid Bug, *Orthezia urticæ* Linn. By ENID N. SIKES, B.Sc. (Plates I. & II.; Text-figures 1–23.) ... 269

15. On Abnormalities in *Rana temporaria* chiefly affecting the Vascular System. By J. H. LLOYD, M.Sc., F.Z.S. (Text-figures 1–7.) 307

Page

16. Some Copepoda from Tanganyika collected by Mr. S. R. B. Pask. By ROBERT GURNEY, D.Sc., F.Z.S. (Text-figures 1–8.) 317

17. The Mallophaga of Sand-Grouse. By JAMES WATERSTON, B.D., D.Sc., F.Z.S. (Text figures 1–10.) 333

18. The Species of *Notogonia* (Hymenoptera, Larridæ) occurring in the Mediterranean Basin. By O. W. RICHARDS, M.A. 357

19. The Morphology of the Cicadidæ (Homoptera). By J. G. MYERS, Sc.D. (Text-figures 1 75.) 365

20. The Larval Stages of the Plymouth Brachyura. By MARIE V. LEBOUR, D.Sc., F.Z.S. (Plates I.–XVI.; Text-figures 1–5.) 473

21. The Morphology of the Isopod Head.—Part II. The Terrestrial Isopods. By H. GORDON JACKSON, D.Sc., F.Z.S. (Text-figures 1 20.) 561

22. The Biology of *Dinocampus* (*Perilitus*) *rutilus* Nees, a Braconid Parasite of *Sitona lineata* Linn.—Part I. By DOROTHY J. JACKSON. (Plates I.–IV.) 597

23. Hints on the Transport of Animals. By Major S. S. FLOWER, O.B.E., V.P.Z.S., and others 631

Alphabetical List of Contributors vii

Index of Illustrations xiii

Index xvii

ALPHABETICAL LIST

OF THE

CONTRIBUTORS,

With References to the several Articles contributed by each.

(1928, pp. 1–660.)

Page

BOULENGER, E. G., F.Z.S. (Director of the Aquarium).

Exhibition of living specimens of *Pipa americana*...... 653

BROWN, Miss E. M. (Aquarium Research Fellow).

Exhibition of Fluke (*Microcotyle* sp.) from the Gills of a Sea Bream (*Pagellus centrodontus*) 653

BUSHBY, L. C., F.E.S. (Curator of Insects). *See* VEVERS, Dr. G. M.

CAMPION, H., and LAIDLAW, F. F., F.Z.S.

Notes on Oriental Dragonflies [Odonata], with Descriptions of New Species. (Text-figures 1–3.)... 129

CHORLEY, C. W., F.Z.S.

Note on Uganda Gorillas 267

CONNOLLY, M.

On a Collection of Land and Freshwater Mollusca from Southern Abyssinia. (Plate I.; Text-figures 1–4.) 163

DUNCAN, F. MARTIN, F.Z.S. (Librarian).

Exhibition of Cinematograph Films taken in the Society's Gardens 268

Exhibition of specimens of Trapdoor Spiders' nests from Queensland, and a female Huntsman Spider (*Heterapoda venatorius*) with her egg-cocoon 653

Page

Elliott, Clarence.
Exhibition of Giant Barnacles from Chile, and of a living specimen of the Giant Tortoise *Testudo microphyes* from Albemarle Island (Galapagos Islands) 658

Flower, Major S. S., O.B.E., F.Z.S.
Exhibition of Photographs taken by Mr. G. C. Flower in the Red Sea 267
Exhibition of living specimen of the Great African Tortoise (*Testudo sulcata*). (Text-figures 1, 2.) 654
—— and others.
Hints on the Transport of Animals.............. 631

Gurney, Robert, D.Sc., F.Z.S.
Some Copepoda from Tanganyika collected by Mr. S. R. B. Pask. (Text-figures 1 8.) 317

Jackson, Dorothy J.
The Biology of *Dinocampus* (*Perilitus*) *rutilus* Nees, a Braconid Parasite of *Sitona lineata* Linn.—Part I. (Plates I.–IV.) 597

Laidlaw, F. F. *See* Campion, H.

Lebour, Marie V., D.Sc., F.Z.S.
The Larval Stages of the Plymouth Brachyura. (Plates I.–XVI ; Text-figures 1–5.).............. 473

Lloyd, J. H., M.Sc., F.Z.S.
On Abnormalities in *Rana temporaria* chiefly affecting the Vascular System. (Text-figures 1–7.)................. 307

Loveridge, Arthur, C.M.Z.S.
Notes on East African Birds (chiefly Nesting-habits and Stomach-contents) collected in 1926.................... 71
Notes on some East African Invertebrates collected in 1926.. 121

Lowe, Percy Roycroft, B.A., M.B., F.Z.S.
Studies and Observations bearing on the Phylogeny of the Ostrich and its Allies. (Plate I. ; Text-figures 1–23.) 185

Page

MAULIK, S., F.Z.S.

New Chrysomelid Beetles from India. With a Note on the Scales of Coleoptera. (Text-figures 1–5.) 151

MITCHELL, Dr. P. CHALMERS, C.B.E., M.A., D.Sc., LL.D., F.R.S. (Secretary to the Society).

Report on the Additions to the Society's Menagerie during the months of October, November, December, 1927, and January, 1928 265

Report on the Additions to the Society's Menagerie during the month of February, 1928 653

Exhibition of Photographs of the Detroit Zoological Gardens 653

Report on the Additions to the Society's Menagerie during the month of March, 1928 658

MONTAGU, The Hon. IVOR, F.Z.S.

Exhibition of Photographs of the Moscow Zoological Gardens 267

MYERS, J. G., Sc.D.

The Morphology of the Cicadidæ (Homoptera). (Text-figures 1–75.) 365

PITMAN, Capt. C. R. S., D.S.O., M.C.

Note on Nkosi Island and its Sitatunga (*Tragelaphus spekii*) 655

RICHARDS, O. W., M.A.

The Species of *Notogonia* (Hymenoptera, Larridæ) occurring in the Mediterranean Basin 357

ROBSON, G. C., M.A., F.Z.S.

Exhibition of lantern-slides illustrating some observations on the oviposition of *Octopus* 267

On the Giant Octopus of New Zealand. (Text-figures 1–6.) 257

Page

ROTHSCHILD, Lord LIONEL WALTER, D.Sc., F.R.S., F.Z.S.
Exhibition of Photographs and Skulls of Gigantic Land Tortoises 658

SCOTT, H. HAROLD, M.D., F.R.C.P., F.R.S Ed., F.Z.S. (Pathologist to the Society).
Carcinoma of the Tonsil in a Common Wolf (*Canis lupus*). (Plates I.–III.) 43
Report on the Deaths occurring in the Society's Gardens during 1927 81
Tuberculosis in Marsupials. (Plates I.–III.) 249

SETH-SMITH, D., F.Z.S. (Resident Curator of Mammals and Birds).
Exhibition of a blue variety of Masked Lovebird (*Agapornis personata*) 266
Exhibition of a lead-pipe gnawed by mice, and Photographs of the Society's New Bird House 653
Exhibition of Photographs of a Pangolin 657

SIKES, ENID K., B.Sc.
The External Morphology and Life-history of the Coccid Bug, *Orthezia urticæ* Linn. (Plates I. & II.; Text-figures 1–23.) 269

SWINNERTON, C. F. M., C.M.Z.S.
Exhibition of Photographs showing forest undergrowth cleared by Sitatunga 657

THOMAS, OLDFIELD, F.R.S.
The Delacour Exploration of French Indo-China.—Mammals. II. On Mammals collected during the Winter of 1926–27 139

VEVERS, Dr. G. M., M.R.C.S., L.R.C.P., F.Z.S. (Superintendent of the Gardens), and BUSHBY, L. C., F.E.S. (Curator of Insects).
Exhibition of specimens of the Mitten Crab (*Eriocheir japonicum*) 267

Page

WATERSTON, JAMES, B.D., D.Sc., F.Z.S.

The Mallophaga of Sand-Grouse. (Text-figures 1–10.). 333

WATSON, Prof. D. M. S., F.R.S., F.Z.S.

On some Points in the Structure of Palæoniscid and allied Fish. (Text-figures 1–15.)............................ 49

ZUCKERMAN, S., M.A. (Anatomist to the Society).

Age-Changes in the Chimpanzee, with special reference to Growth of Brain, Eruption of Teeth, and Estimation of Age: with a Note on the Taungs Ape. (Plates I.–IV.; Text-figures 1–3.) 1

ZOOLOGICAL SOCIETY OF LONDON.

INSTRUCTIONS TO AUTHORS.

Owing to the cost of printing, the Publication Committee beg to draw the attention of Authors submitting papers for publication by the Society to the following Regulations. If the conditions are not observed, papers may have to be returned :—

1. MSS. submitted for publication must be written in a clear and legible handwriting, or, preferably, be type-written, and must be in final form for printing. The MSS. should be written on one side of each sheet only, and the pages clearly numbered, All tables of contents, references to plates, or legends to illustrations in the text, etc., must be in their proper places, **with page and plate numbers left blank**; and the position for the text figures must be indicated. References to literature must be exact, with the page number as well as the volume number and date.

Contributors of papers involving extensive numerical observations are requested to consult the recommendations of the British Association Committee on Biological Measurements 1927, obtainable from the British Association, Burlington House, W. 1, price *6d.*

Arrangements have been made whereby original data, too extensive for complete publication, may be deposited at the British Museum (Natural History) or with the Royal Society of Edinburgh, and so be made available for future workers. Authors desirous of depositing data, whether zoological or botanical, in this manner should communicate with either the Keeper of Zoology, Natural History Museum, S.W. 7, or the General Secretary, The Royal Society of Edinburgh, 22 George Street, Edinburgh, enclosing full bibliographic reference to the publication in which the results are summarised.

2. Proofs and their Correction.—Two copies of the slip proof, and a page proof for final revision, will be sent to the Author, **but it is important that all serious corrections be made on the slip proof.** Expenses for proof corrections are very heavy, but, if the MSS. comply with Regulation 1, should not exceed 25 per cent. of the printers' charges. If the cost of corrections exceeds 25 per cent., a proportion of the excess will be charged to the Author.

3. Revised proofs must, if possible, be returned within one week from the date of their receipt by the Author.

4. The Author receives 30 copies of reprints free, and, with the sanction of the Publication Committee, may obtain leave to buy extra copies, at the cost price charged by the printers and engravers to the Society. The number of separate copies required must be stated when returning the proof.

5. ILLUSTRATIONS.—Drawings intended to be reproduced as line-block text-figures should be drawn with a good black ink, such as "Process Black" or the best "Indian ink" on white "Bristol board." All lines and dots must be clear and sharp, and no washes or colours used. Wash drawings are not suitable for reproduction as text-figures. All necessary lettering **must be clearly, but lightly, indicated in pencil,** so that the engravers may insert sharp, well-drawn letters. Each drawing should be numbered to tally with the text-figure number given in the MSS., and be accompanied by a short, concise, and legible descriptive legend. When making drawings for text-figures, or grouping drawings, it should be borne in mind that, when reduced, the figures must not exceed the dimensions of the printed matter on the page of "Proceedings," viz.: - 3½ × 6¼ inches. Drawings or photographs intended for reproduction as plates will have to be reduced, when necessary, to fit a space of 4½ × 7 inches.

6. COPYRIGHT.—No use whatever is permitted of the type or illustrations prepared for the Society's Publications other than for the Separate Copies mentioned above, unless the leave of the Committee has been obtained, and recorded on the Minutes. Permission is given only with the consent of the Authors of the papers, if alive, and the source of the text and illustrations shall be stated in the work in which they are used. The use of illustrations from the Society's Publications, if within five years of the date of publication, will be granted only upon the payment of half the cost of their production. All communications made to the Society shall, if accepted for publication, be regarded as the property of the Society, and not returned to the Authors, except for the purpose of comparison with the proof when set up in type.

Note.—The Publication Committee is always ready to give Authors who apply for it, permission to reproduce matter that they have contributed to the Society's "Proceedings" and "Transactions," but the Society has been advised that a formal assignment from Authors is necessary to enable it to protect copyright against third parties.

ZOOLOGICAL SOCIETY OF LONDON.

This Society was founded in 1826 by Sir Stamford Raffles, Mr. J. Sabine, Mr. N. A. Vigors, and other eminent Naturalists, for the advancement of Zoology and Animal Physiology, and for the introduction of new and curious subjects of the Animal Kingdom, and was incorporated by Royal Charter in 1829.

Patron.

HIS MAJESTY THE KING.

COUNCIL.

HIS GRACE THE DUKE OF BEDFORD, K.G., F.R.S., *President.*

Sir John Bland-Sutton, Bt., F.R.C.S.

Charles Drummond, Esq., *Treasurer.*

Alfred Ezra, Esq., O.B.E.

The Rt. Hon. The Viscount Grey, K.G., P.C., F.R.S., *Vice-President.*

Prof. James P. Hill, D.Sc., F.R.S., *Vice-President.*

Major Stanley S. Flower, O.B.E., F.L.S., *Vice-President.*

Lt.-Col. The Lord Alastair Innes-Ker, D.S.O.

Sir Walter R. Lawrence, Bt., G.C.I.E., G.C.V.O.

J. Spedan Lewis, Esq.

Professor Ernest William MacBride, M.A., D.Sc., F.R.S., *Vice-President.*

Col. Sir A. Henry McMahon, G.C.V.O., G.C.M.G., K.C.I.E., C.S.I.

Henry G. Maurice, Esq., C.B.

Edmund G. B. Meade-Waldo, Esq.

P. Chalmers Mitchell, Esq., C.B.E., M.A., D.Sc., LL.D., F.R.S., *Secretary.*

The Rt. Hon. The Earl of Onslow, P.C., O.B.E., *Vice-President.*

Major Albert Pam, O.B.E.

Lt.-Col. Sir David Prain, C.M.G., C.I.E., F.R.S.

Richard S. Taylor, Esq.

Anthony Henry Wingfield, Esq., D.L.

Sir Arthur Smith Woodward, LL.D., F.R.S., *Vice-President.*

The Society consists of Fellows, Imperial Fellows, Honorary, Foreign, and Corresponding Members, elected according to the By-Laws. It carries out the objects of its foundation by means of its collection of living animals, by its Library, and by its Scientific Publications.

The Office of the Society, Regent's Park, N.W.8, where all communications should be sent, addressed to "The Secretary," is open from Ten till Five, except on Saturdays, when it closes at ONE P.M.

The Library, under the superintendence of Mr. F. Martin Duncan, F.R.M.S., F.R.P.S., F.Z.S., is open daily (except Sunday) from Ten A.M. till Five P.M.; on Saturdays, Ten A.M. till One P.M.

The Library is closed from Good Friday to Easter Monday, and upon all other Bank Holidays. It is also closed annually for cleaning during the month of September.

The Meetings of the Society for General Business are held in the Meeting Room at the Society's Office on the third Wednesday of the month at 4.30 P.M. except in September and October.

The Meetings for Scientific Business are held in the Meeting Room at the Society's Office fortnightly on Tuesdays, except in July, August, September, and December and January, at half-past Five o'clock P.M.

The Anniversary Meeting is held on the 29th of April, or the nearest convenient day, at Four P.M.

The Society's Gardens are open daily from Nine o'clock until Sunset, or 8 P.M. when sunset is later. Dr. G. M. Vevers is the Superintendent, Mr. D. Seth-Smith, Curator of Mammals and Birds; Mr. Edward G. Boulenger is Director of the Aquarium; Miss Joan B. Procter, F.L.S., is Curator of Reptiles; Mr. L. C. Bushby, F.E.S., is Curator of Insects; Mr. S. Zuckerman, M.A., is Anatomist; Dr. H. H. Scott, M.D., F.R.C.P., D.P.H., Pathologist; Prof. R. T. Leiper, F.R.S., with the assistance of a panel of experts, examines and reports on the Parasites; Prof. G. H. Wooldridge, F.R.C.V.S., is Honorary Consulting Veterinary Surgeon; and Dr. R. W. A. Salmond, O.B.E., Honorary Radiologist to the Society. Applications for anatomical or pathological material, or for facilities for work in the Prosectorium should be addressed to the Secretary.

TERMS FOR THE ADMISSION OF FELLOWS.

FELLOWS pay an Admission Fee of £5, and an Annual Contribution of £3, due on the 1st of January, and payable in advance, or a Composition of £45 in lieu thereof; the whole payment, including the Admission Fee, being £50.

No person can be deemed a FELLOW until the Admission Fee and first Annual Subscription of £3 have been paid, or the annual payments have been compounded for.

The usual Admission Fee of £5 is waived upon the election of the WIFE or HUSBAND of an existing FELLOW.

The First Annual Subscription of Fellows elected in November and December covers the following year.

PRIVILEGES OF FELLOWS.

Fellows have Personal Admission to the Gardens upon signing their names in the book at the entrance gate, and may introduce Two Companions daily.

The Wife or Husband of a Fellow can exercise these privileges in the absence of the Fellow, but this privilege cannot be extended to children of Fellows.

Until further notice, Fellows will receive 40 undated Green Cards, available on any Sunday or week-day up to the end of February of the year following the year of issue, and 20 White Cards available on any week-day up to the same date. Special children's tickets are no longer issued, but the Green and White Cards are perforated, and each half is valid for a Child under twelve years of age. Additional Sunday tickets cannot be purchased or acquired. It is particularly requested that Fellows *will sign every ticket* before it goes out of their possession. Unsigned tickets are not valid.

Fellows are not allowed to pass in friends on their written order or on presentation of their visiting cards.

Aquarium.—Fellows have free personal admission to the Aquarium at all times when it is open. On Sundays, but not on week-days, they may introduce two visitors with them. These privileges are personal and cannot be transferred. For admission to the Aquarium of other friends whom they have admitted to the Gardens by Sunday tickets they may purchase from the Office books of 20 tickets for £1, or a smaller number at the same rate, each ticket admitting one adult or two children on Sundays or week-days. Fellows may also purchase a transferable Aquarium Ivory Ticket, for £10, valid for the whole duration of the Fellowship and admitting daily, on Sundays or week-days, two persons who have already gained admission to the Gardens.

Fellows have the privilege of receiving the Society's ordinary Publications issued during the year upon payment of the additional Subscription of One Guinea. This Subscription is due upon the 1st of January, and must be paid before the day of the Anniversary Meeting, after which the privilege lapses. Fellows are likewise entitled to purchase these Publications at 25 per cent. less than the price charged to the public. A further reduction of 25 per cent. is also made upon all purchases of Publications issued prior to 1881, if above the value of Five Pounds.

Fellows also have the privilege of subscribing to the Annual Volume of 'The Zoological Record,' which gives a list of the Works and Publications relating to Zoology in each year, for the sum of Two Pounds Ten Shillings. Separate divisions of volumes 39 onwards can also be supplied. Full particulars of these publications can be had on application to the Secretary.

Fellows may obtain a Transferable Ivory Ticket admitting two persons, available throughout the whole period of Fellowship, on payment of Ten Pounds in one sum. A second similar ticket may be obtained on payment of a further sum of Twenty Pounds.

Any Fellow who intends to be absent from the United Kingdom during the space of at least one year, may, upon giving to the Secretary notice in *writing*, have his or her name placed upon the "dormant list," and will then be called upon to pay an annual subscription of £1 only during such absence, or in the event of returning to the United Kingdom before June 30th in any year to pay the balance of the ordinary subscription. After three years a Dormant Fellow must make a further application to be retained on that list.

Any Fellow, having paid all fees due to the Society, is at liberty to withdraw his or her name upon giving notice in *writing* to the Secretary.

Ladies or Gentlemen wishing to become Fellows of the Society are requested to communicate with "The Secretary."

P. CHALMERS MITCHELL,
Secretary.

Regent's Park, London, N.W. 8.
June, 1928.

MEETINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON

FOR

SCIENTIFIC BUSINESS.

1928.

Tuesday, October .... 23.

——— November .... 6 and 20.

The Chair will be taken at half-past Five o'clock precisely.

ZOOLOGICAL SOCIETY OF LONDON.

LIST OF PUBLICATIONS.

The scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in an octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication A large number of coloured plates and engravings are issued in the volumes of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described therein. Amongst such illustrations, figures of the new or rare species acquired in a living state for the Society's Gardens are often given.

The "Proceedings" for each year are issued in four parts, paged consecutively, during the months of March, June, September, and December. From January 1901 they have been issued as two half-yearly volumes, indexed separately.

An "Abstract of the Proceedings" is published by the Society on the Tuesday following the date of the Scientific Meeting to which it refers. It is issued along with the "Proceedings," free of extra charge, to all Fellows who subscribe to the Publications, but it may be obtained on the day of publication at the price of Sixpence, or, if desired, sent post free for the sum of Six Shillings per annum, payable in advance.

The "Transactions" contain such of the communications made to the Scientific Meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of One Guinea *before* the day of the Anniversary Meeting, are entitled to receive the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 25 per cent. less than the price charged to the Public. A further reduction of 25 per cent. is made upon purchases of Publications issued prior to 1881, if they exceed the value of Five Pounds.

Fellows also have the privilege of subscribing to the Zoological Record for a sum of Two Pounds Ten Shillings (which includes cost of delivery), payable on the 1st of July in each year; but this privilege is forfeited unless the subscription be paid *before* the 1st of December following.

The following is a complete list of the publications of the Society already issued.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

4to. 20 vols. and Index.					Price to Fellows.	Price to the Public.
Vols. I.-IV. (out of print).						
Vol.	V.,	containing 67	Plates	(1862-66)	5 4 3	6 19 0
„	VI.,	„ 92	„	(1866-69)	11 5 0	15 0 0
„	VII.,	„ 73	„	(1869-72)	10 4 0	13 12 0
„	VIII.,	„ 82	„	(1872-74)	9 8 3	12 11 0
„	IX.,	„ 99	„	(1875-77)	12 1 6	16 2 0
„	X.,	„ 95	„	(1877-79)	10 0 3	13 7 0
Index, Vols. I.-X.				(1833-79)	0 7 6	0 10 0
Vol.	XI.,	containing 97	Plates	(1880-85)	9 12 0	12 16 0
„	XII.,	„ 65	„	(1886-90)	5 8 0	7 4 0
„	XIII.,	„ 62	„	(1891-95)	6 8 3	8 11 0
„	XIV.,	„ 47	„	(1896-98)	5 5 0	7 0 0
„	XV.,	„ 52	„	(1898-1901)	5 15 6	7 14 0
„	XVI.,	„ 38	„	(1901-1903)	5 8 0	7 4 0
„	XVII.,	„ 41	„	(1903-1906)	5 18	7 18 0
„	XVIII.,	„ 43	„	(1907-1911)	4 1 0	5 8 0
„	XIX.,	„ 24	„	(1909-1910)	10 4 0	13 12 0
„	XX.,	„ 53	„	(1912-1915)	11 10 3	15 7 0
„	XXI.—Part I. (7 Plates & 12 Text-figs.)			(June 1916)	2 5 0	3 0 0
„	XXII.—Part I. (Text-figures 1-13)			(December 1926)	1 17 6	2 10 0
„	„ —Part II. (Text-figures 14-76)			(March 1927)	1 17 6	2 10 0
„	„ —Part III. (Text-figures 77-104)			(July 1927)	1 17 6	2 10 0
„	„ —Part IV. (Text-figures 105-168)			(December 1927)	1 17	2 10 0

In consequence of a re-arrangement of the stock of the 'Transactions,' the Society is now able to offer for sale, at the reduced price of £30, sets of Vols. V.-XVI. inclusive.

PROCEEDINGS OF THE COMMITTEE OF SCIENCE AND CORRESPONDENCE OF THE ZOOLOGICAL SOCIETY OF LONDON. 8vo. 2 vols. (Letterpress only).

			Price to Fellows.	Price to the Public.
Part I.	**1830-31.**	**1 vol. 8vo., out of print.**		
„ II.	**1832.**	**„**	***4s. 6d.***	***6s.***

PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON.

FIRST SERIES.

Parts I.–XV. (1833–1847). 8vo. 15 vols. (Letterpress only.) Price to Fellows : 4*s*. 6*d*. each part ; to the Public, 6*s*.

Index 1830–1847. Price to Fellows : 4*s*. 6*d*. ; to the Public, 6*s*.

Parts I., VII.–IX., XI., XIV., XV., out of print.

SECOND SERIES.

Parts XVI.–XXVIII. (1848–1860). 8vo. 13 vols. (Letterpress only.) Price to Fellows : 4*s*. 6*d*. each part ; to the Public, 6*s*.

Index 1848–1860. Price to Fellows : 4*s*. 6*d*. ; to the Public, 6*s*.

The Parts of this series containing Coloured Plates are out of print.

PROCEEDINGS OF THE SCIENTIFIC MEETINGS OF THE ZOOLOGICAL SOCIETY OF LONDON. 8vo.

	Letterpress only.		With Plates uncoloured.		With Plates coloured.	
	Price to Fellows.	Price to the Public.	Price to Fellows.	Price to the Public.	Price to Fellows.	Price to the Public.
1861	4*s*. 6*d*.	6*s*.	9*s*.	12*s*.	33*s*. 9*d*.	45*s*.†
1862	4*s*. 6*d*.	6*s*.	9*s*.	12*s*.	33*s*. 9*d*.	45*s*.†
1863	4*s*. 6*d*.	6*s*.	9*s*.	12*s*.	33*s*. 9*d*.	45*s*.†
1864	4*s*. 6*d*.	6*s*.*	9*s*.	12*s*.†	33*s*. 9*d*.	45*s*.*
1865	4*s*. 6*d*.	6*s*.†	9*s*.	12*s*.	33*s*. 9*d*.	45*s*.
1866	4*s*. 6*d*.	6*s*.†	9*s*.	12*s*.†	33*s*. 9*d*.	45*s*
1867			9*s*.	12*s*.*	33*s*. 9*d*.	45*s*.
1868			9*s*.	12*s*.	33*s*. 9*d*.	45*s*.
1869			9*s*.	12*s*.	33*s*. 9*d*.	45*s*.
1870			9*s*.	12*s*.	33*s*. 9*d*.	45*s*.
Index, 1861–1870			4*s*. 6*d*.	6*s*.		
1871			9*s*.	12*s*.*	33*s*. 9*d*.	45*s*.†
1872			9*s*.	12*s*.*	33*s*. 9*d*.	45*s*.†
1873			9*s*.	12*s*.	33*s*. 9*d*.	45*s*.†
1874			9*s*.	12*s*.†	36*s*.	48*s*.†
1875			9*s*.	12*s*.	36*s*.	48*s*.
1876			9*s*.	12*s*.	36*s*.	48*s*.†
1877			9*s*.	12*s*.	36*s*.	48*s*.
1878			9*s*.	12*s*.	36*s*.	48*s*.
1879			9*s*.	12*s*.	36*s*.	48*s*.
1880			9*s*.	12*s*.	36*s*.	48*s*.
Index, 1871–1880			4*s*. 6*d*.	6*s*.		
1881-1890. Ten volumes			Each		36*s*.	48*s*
Index, 1881–1890			4*s*. 6*d*.	6*s*.		
1891–1900. Ten volumes			Each		36*s*.	48*s*.
Index, 1891–1900			4*s*. 6*d*.	6*s*.		

*** No perfect copies in stock.** **† Out of print.**

PROCEEDINGS OF THE GENERAL MEETINGS FOR SCIENTIFIC BUSINESS OF THE ZOOLOGICAL SOCIETY OF LONDON

(*continued*).

	Price to Fellows.	Price to the Public
1901–1910.* Twenty volumes	Each 18*s*.	24*s*
Index, 1901–1910	4*s*. 6*d*.	6*s*.
Index, 1911–1920	8*s*.	10*s*.
1911–1916.† Twelve volumes	18*s*.	24*s*.
1917. Vol. I.	18*s*.	24*s*.
„ „ II.	9*s*.	12*s*.
1918. Two volumes	9*s*.	12*s*.
1919. Two volumes	15*s*.	20*s*.
1920. Vol. I.	15*s*.	20*s*.
„ „ II.	18*s*.	24*s*.
1921. Two volumes	18*s*.	24*s*.
1922. Two volumes	18*s*.	24*s*.
1923. Two volumes	18*s*.	24*s*.
1924. Two volumes	18*s*.	24*s*.
1925.‡ Two volumes	18*s*.	24*s*.
1926. Two volumes	18*s*.	24*s*.
1927. Two volumes	18*s*.	24*s*.

* 1908 out of print. † 1911 out of print.
‡ 1925, Vol. I., out of print.

CATALOGUE OF THE LIBRARY of the Zoological Society of London (Fifth Edition.) 8vo. 1902. Cloth, 6*s*.

THE OFFICIAL ILLUSTRATED GARDEN GUIDE—25th Edition (Revised)—with (1) a Railway and Street Map; (2) a Plan of the Grounds; (3) a short description of some of the principal animals in the Collection, with 57 Photographic Illustrations and Index. Price 1*s*. in Stiff Paper Cover, postage 2*d*.

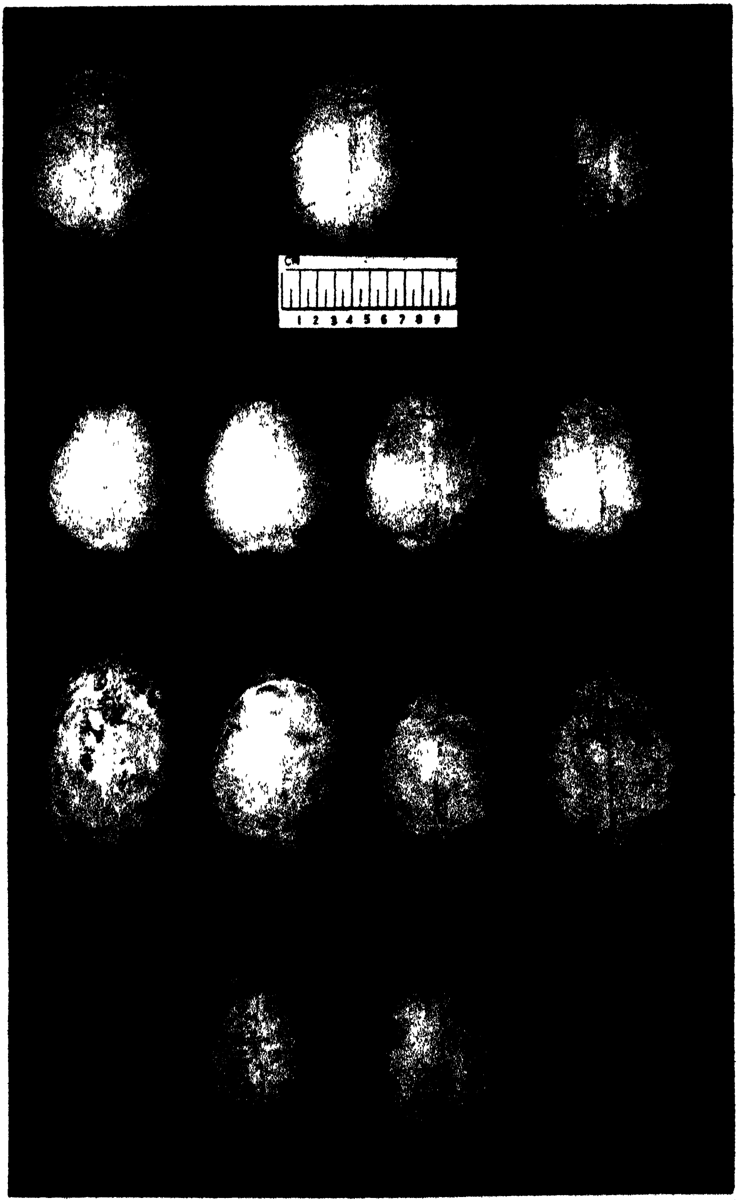
ILLUSTRATED GUIDE TO THE AQUARIUM. Price 6*d*., postage 2*d*.

ZOOLOGICAL RECORD.—Vol. 63, containing literature relating chiefly to the year 1926, has now been published, price £3. Vol. 64, for the year 1927, is being prepared as usual, price £3, or subscription, if paid in advance, £2 10*s*. 0*d*.

P. CHALMERS MITCHELL,
Secretary.

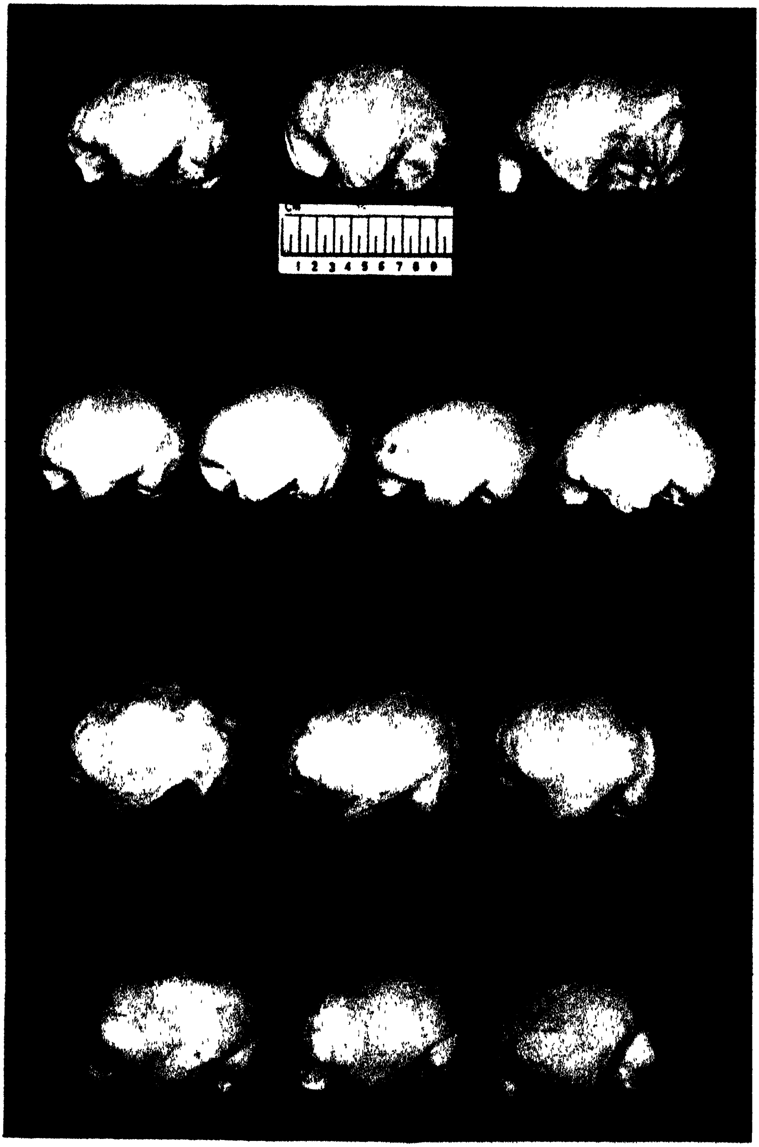
Regent's Park, London, N.W. 8.
June 1928.

These publications may be obtained at the SOCIETY'S OFFICE *or through any bookseller.*



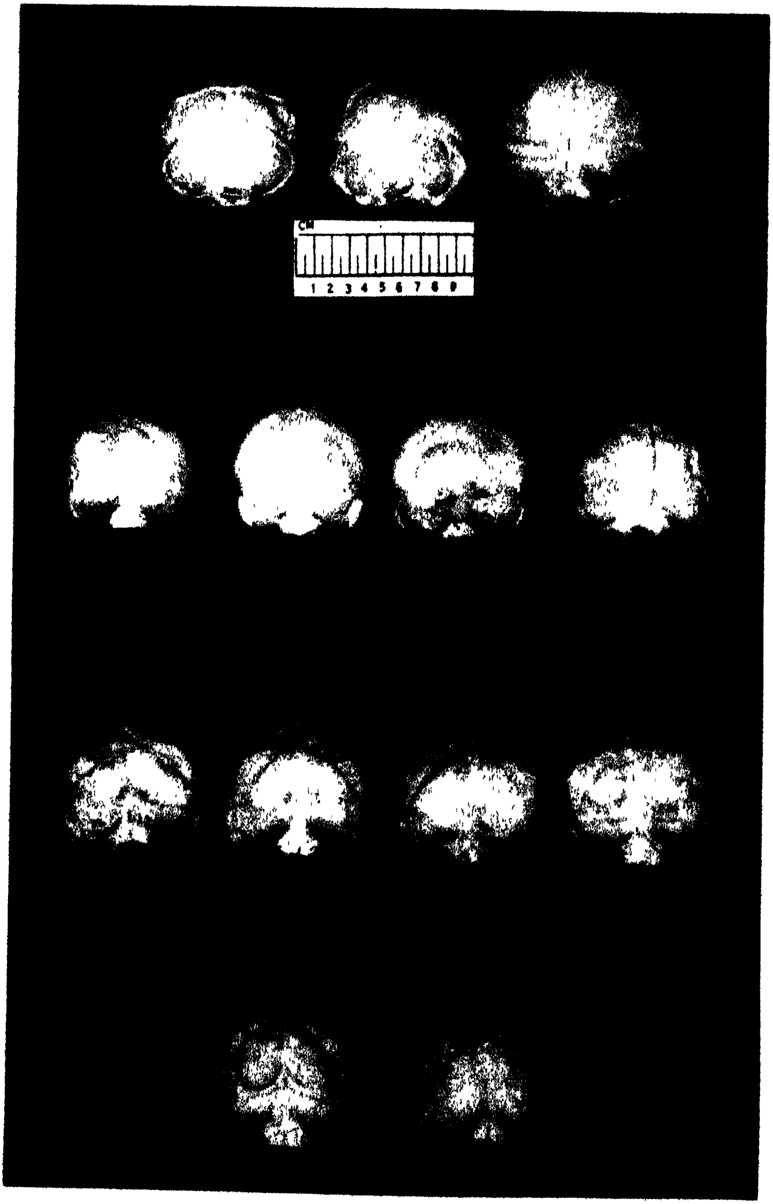
John Bale Sons & Danielsson, L^td

AGE CHANGES IN THE CHIMPANZEE



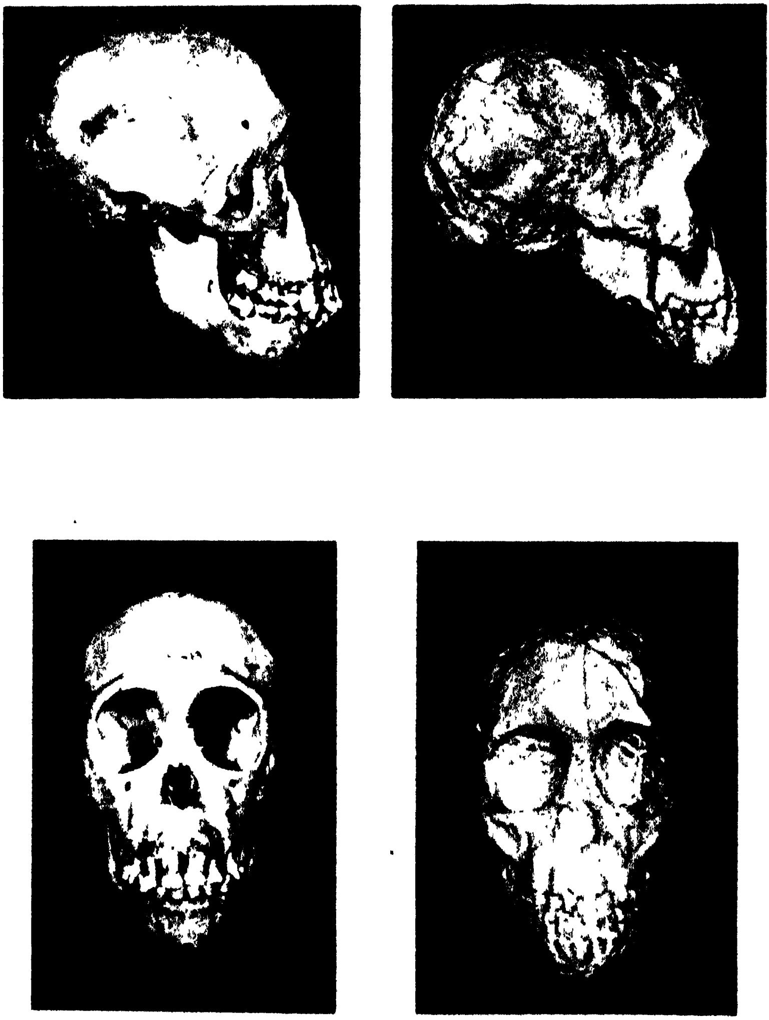
John Bale, Sons & Danielsson, L^td

AGE CHANGES IN THE CHIMPANZEE.



John Bale, Sons & Danielsson, Ltd

AGE CHANGES IN THE CHIMPANZEE



John Bale Sons & Danielsson L.td

AGE CHANGES IN THE CHIMPANZEE

PROCEEDINGS

OF THE

GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

OF THE

ZOOLOGICAL SOCIETY OF LONDON

PAPERS.

1. Age-changes in the Chimpanzee, with special reference to Growth of Brain, Eruption of Teeth, and Estimation of Age; with a Note on the Taungs Ape.

By S. ZUCKERMAN *, M.A., Institute of Anatomy, University College, London †.

CONTENTS.

	Page
1. Introduction	1
2. Material and Technique	3
3. The Exterior of the Cranium	10
4. Cranial Capacity	13
5. Endocranial Casts	18
6. Eruption of the Teeth	21
7. Endocranial Volume and Brain Volume	28
8. The Contrast between Human and Anthropoid Brain-growth	33
9. The Taungs Ape	35
10. Summary	38
11. Literature	40

[Received November 7, 1927 : Read February 7, 1928.]

(Plates I.-IV.‡; Text-figures 1-3.)

1. INTRODUCTION.

In a communication to the Proceedings of the Zoological Society (1926), I summarized earlier views on anthropoid brain-growth as follows:—"Keith (1910) writes: 'The age-changes in the anthropoid skull have little or nothing to do with the brain-growth, for by the end of the first year, if not earlier,

---

* Now Anatomist to the Society.

† Communicated by Prof. G. ELLIOT SMITH, F.R.S., F.Z.S.

‡ For explanation of the Plates, see p. 42.

their brains cease to grow.' Virchow (quoted by Macnamara, 1902) states that the Ape's brain reaches perfection before the shedding of the teeth, and ceases to grow at this stage. Duckworth (1915) similarly writes: 'That nothing is more impressive in the Gorilla than the small amount of brain-growth after infancy.' Topinard (1867), however, records an increase of 22 per cent. of the cranial capacity in the Orang between the period of the eruption of the permanent teeth and maturity."

Keith (1910) further states that the cranial capacity in large anthropoids actually decreases with age, and the decrease affects the vertical diameter of the skull measured from the upper surface of the presphenoid to the internal bregma. This statement is qualified by Duckworth (1915), who writes that, "even if actual diminution of the vaulting is demonstrable, the arrest or diminution is not absolute, ... and compensation takes place by way of an increase in transverse width."

Finding that certain young anthropoid skulls which I examined had capacities well below the limit to be expected, provided that the views expressed above were correct, and having myself been able to demonstrate growth in the Baboon's brain after milk dentition, I suggested that the question of anthropoid brain-growth demanded re-investigation. A striking instance of this need was evidenced by the discovery of the Taungs skull. In the lively controversy which followed, the size of its brain and its probable development were widely discussed, and authorities differed greatly in regard to the amount of growth which takes place in the anthropoid brain after the first permanent molar has erupted.

I have since found two further references to a cessation of brain-growth in Anthropoids earlier than it occurs in Man. Hagedoorn (1924), after an examination of a large number of skulls, did not feel justified in saying that the anthropoid cranial capacity increases during the eruption of the permanent teeth; and Anthony and Coupin (1926) are under the impression that the anthropoid brain stops growing between two and three years.

On the other hand, Keith, in 1895, gave the brain-weights of seventeen Chimpanzees taken from fifteen sources in the literature, and twelve cranial capacities from five sources; he also gave similar collected data for thirty-eight Gorillas and eleven Orangs. The combination of the results of so many observers is an unreliable method of arriving at a generalisation; nevertheless, his conclusion was that, when the Chimpanzee was five years old (*i. e.*, one year after the first permanent molar had erupted), its brain volume was only 90 per cent. of the adult volume. The Orang's brain reached this figure at ten years, and the Gorilla's at three. In the recent discussion on the Taungs skull (1925), Keith referred back to this work and allowed the Taungs Ape 15 per cent. increase in cranial capacity before adult proportions were reached. Keith's statement of 1910, that his "observations show that the maximum size is reached much earlier in anthropoids—probably before the middle of the second year, when the milk dentition is completed," does not, therefore, conform with his 1895 work, to which he has referred in connection with *Australopithecus*.

Bischoff (1867) gave the cranial capacities of eight Chimpanzees; the younger skulls have capacities well below those of the adults (see Table III. p. 14). In Virchow's 1880-1883 papers there is no evidence for the view that the anthropoid brain ceases to grow "before the shedding of the teeth." Selenka's (1898) observations showed that the growth of the brain-box followed the same course in all the anthropoids. After the completion of the milk dentition the cranial capacity was 80-86 per cent. of its adult size, and after the eruption of the second permanent molar had reached 94–97 per cent. On account of the small number of young skulls which he examined, he did not express himself with certainty.

Oppenheim (1911) gave as his opinion that growth in the anthropoid brain continued long after the last permanent molar had erupted, and terminated only when the sutures were obliterated. "Die definitive Grösse der Kapazität des Schimpansen scheint mit dem Abschluss der zweiten Dentition noch nicht erreicht zu sein, da die Nähte des Gehirnschädels sich länger offen erhalten." Oppenheim's view, though based upon as much evidence as supports any other, has attracted little attention in the literature.

The idea peculiar to most of these opinions is that at some stage in the maturation of the anthropoids there is an abrupt cessation of brain-growth. This stage, apparently, is to be defined within narrow limits, the process operating in all individuals. Donaldson (1895) warns us against interpreting the "general" method of growth-estimation in this way. "Observations made on the growth of any part made by the 'general' method are of little use in determining the age at which growth in the individual ceases, because, so long as any of the individuals grow, the curve will rise, and there is no way to determine whether the rise is due to a slight growth in many, or a greater growth in a few." The latter principle has been adopted as that which operates in the growth of the human brain, while the former seems to have been relegated to the anthropoids. It is my opinion that there is as much variability in the time of growth-cessation in the higher apes as occurs in Man. To this, as well as to paucity of material, can be attributed the varying views mentioned above.

2. Material and Technique.

To throw further light on the problem, an investigation was carried out on 112 Chimpanzee skulls, forty of which were immature. Of the 112 only ninety-seven were in a condition which permitted the estimation of their cranial capacities.

No attempt was made to subdivide them into varieties, although at different times several have been described. There are, however, two well-marked species, the common Chimpanzee and the bald-headed form, and the latter is said (Sonntag, 1924) to have a more elevated skull. Kohler (1925) remarks that "we are far from possessing a clear and systematised classification of the varieties of the Chimpanzee." Selenka (1898) found in the Orang a racial variation in cranial capacity; but, though he mentions varieties of Chimpanzee, he groups them as one in his estimations. Hagedoorn (1924) denies the existence of any racial factor in the variability of cranial capacity, and attributes it entirely to age and individual characteristics.

As the geographical sources of the skulls in the series I examined were, in the majority of cases, not indicated, no possible racial factor could be considered. It seems unprofitable also, in the present state of our knowledge, to attempt any classification of Chimpanzees on the form of their skulls alone, especially in view of the extreme variability which they exhibit. For the present purpose, therefore, all the skulls which I examined have been treated as belonging to a single species.

I wish to express my indebtedness to Professor Sir Arthur Keith, the Conservator of the Museum of the Royal College of Surgeons; to Mr. W. P. Pycraft, of the British Museum of Natural History, South Kensington; and to Dr. John Beattie, lately Anatomist to the Zoological Society, for allowing me to examine the material in their care. Mr. Pycraft very kindly gave me permission, while working at the Natural History Museum, to avail myself also of the opportunity of studying a number of skulls belonging to Lord Rothschild, which were on loan at the Museum at the time.

Ageing and Sexing of Skulls.

As a rule there is no difficulty in distinguishing between the adult male and adult female skulls, and only in one or two cases was there a little doubt as to the correct sex. The main distinguishing features are the teeth, particularly the canines, and the larger size of the male as a whole. The average prosthion inion diameter in the male is 192·5 mm., range 180–207, and in the female 183·5 mm., range 164–201. A sagittal crest develops in the male in only 10 per cent. of cases, so that this usual distinguishing mark between the sexes in adult anthropoids is little help where the Chimpanzee is concerned.

The problem is entirely different when one comes to consider skulls of milk dentition and those which have only the first molar of the permanent dentition erupted. Here there is very little to help when attempting to discover the sex of the skulls. Unfortunately, too, museum records of Primate collections seldom extend so far as sex and age. To meet this difficulty, very careful measurements were made of the skull and of the deciduous teeth in three cases where the sex was recorded. Having taken similar measurements in the other skulls, it was found possible to divide the unknown skulls into sex-groups. This is without doubt an unsatisfactory method, so, as far as possible, these young skulls will be considered irrespective of sex.

Estimating the age of the skulls is very difficult, as little is known of the times of eruption of the teeth. The known data indicate, as I shall show at a later stage in this paper, that these times are much the same as in Man. Meanwhile, the juvenile skulls have been arranged for the tables according to their dentition, and, in the separate classes thus made, according to gradations in age as seen by comparing one skull with another. This is the method followed by all previous workers: Selenka (1898), in the Orang, and Hagedoorn (1924), in the three anthropoids, have divided the group with milk dentition and first permanent molar into subgroups, such as "just erupting" and "erupted." In two of the Chimpanzees now living in the Zoological Gardens the eruption of the first molar, from the moment the tooth appeared above the alveolar margin until it was in place, took about four months. The subdivision, therefore, seems to me to be a useless procedure.

The adult skulls have been arranged in the tables by reference to the criteria of maturity: *i.e.* (1) Condition of the spheno-basilar suture, (2) Condition of the other cranial and facial sutures, and (3) The wear of the teeth. Very few of the adult skulls were found to have the spheno-basilar suture unclosed; Duckworth (1904), 'Studies in Anthropology,' records the unclosed condition as a frequent occurrence in the adult Gorilla, and such, too, were my findings in regard to the Baboon (1926). It may be noted here that the exoccipitals, basioccipital, and supraoccipital are generally separate in skulls of milk dentition. Fusion of the basioccipital with the exoccipitals occurs about the time the first permanent molor erupts, while the supraoccipital joins somewhat later, after the tooth is in place. About this time, too, the maximum transverse diameter of the skull commences to descend from the parietals, and before long the bimastoid is the widest diameter of the skull. The metopic suture closes about the time of completion of the milk dentition, although it is still present in one skull in which the first permanent molar has erupted. The vault sutures commence to fuse generally about the time the third molars erupt.

Technique in Estimation of Cranial Capacities.

The capacities were estimated with lead-shot following the method of tight packing. The volume of the shot used was ascertained by pouring it into an ordinary measuring cylinder and compressing as much as possible. The mean of three readings was taken for each skull. Subsequently endocranial casts of twelve skulls were made, and exact values for their capacities so obtained (see p. 19). Comparison with the shot-method figures showed an average error of 2·2 per cent. (average absolute error 7 c.c.). The shot-values as a rule are too high (see Table IV. p. 19).

About a year later I re-estimated the capacities of three skulls with the shot-method to see how these later readings would compare with the earlier. They were in all three higher, by 12 c.c., 7 c.c., and 4 c.c. respectively, the difference varying from 1 to 3½ per cent. of my former readings.

The absolute variations are small compared with those found when employing practically any method in human craniometry (Wingate Todd, 1923). This is due to the small size of the Chimpanzee endocranium; the absolute error no doubt varies with the size of the cavity to be measured, the relative variation being about the same. Until a completely uniform method of cranial capacity estimation is used by all, the estimations of one observer should not be directly compared with those of another. Generalisations, such as have frequently been made in the past, from the combined data of different workers must necessarily be unsound. The general conclusions of one observer, however, can profitably be compared with those of another.

External Measurements of Skull.

Until the first permanent molar has erupted, the maximum transverse diameter of the skull is taken on the parietals or on the upper limits of the squamous temporal. After this stage the mastoid air-cells commence to develop and the bimastoid becomes the greatest transverse diameter of the skull. Two diameters were therefore estimated in these older skulls, the bimastoid and one taken on the lowest part of the squamous temporal just before it merges with the mastoid projection (see p. 10). Oppenheim used the distance from one euryon to the other as the transverse diameter of the skull. By euryon he meant the upper limit of the squamous temporal. Selenka measured the distance between two points just above the mastoid projection—about 3½ to 4 cm. above the upper limit of the external auditory meatus. Actually, as Harris has pointed out (1926, see p. 10), this diameter is a very variable one, and the greatest width is only found with difficulty. The minimum frontal diameter was taken on the frontal-alisphenoid articulation in the temporal fossa.

Table I.

"CA," University College. "RCS," Royal College of Surgeons. "NH," Natural History Museum. "R," Rothschild. "Z," Zoological Society, London. "?" following cranial capacity figures indicates that the cranium was broken and incomplete, making the readings slightly uncertain.

Part I.

Subadults.

No. of Skull.	Description.	Cranial Capacity.	Maximum Ant. Post. Diam.	Max. Transverse Diameter.	Bismatoid Diameter.	Min. Frontal Breadth.	Basion Bregmatic Height.	Auriculo-Bregmatic Height.
RCS 16	♂ Metopic suture open. 2nd milk molars and canines erupting.	—	100	89	—	57	73	66
NH 2 *a*	♀ Milk canines erupting	340	107	92	—	57	78·5	72
RCS 18 A	♀ Acrocephalic deformity. Coronal and most of sagittal sutures occluded. Lower canines not quite erupted.	340	106	89	—	61·5	87	74
RCS 17	♀ Complete milk dentition	270	99·5	87	—	58	71·5	64
Z 3	♂ Complete milk dentition	340	110	94	—	61	78	70
CA 14 *d*	♂ ,, ,, ,,	295	105	88	—	61	75·5	70
NH 2 *b*	♂ ,, ,, ,,	350	112	94	—	60	82	74
RCS 17.3	♀ ,, ,, ,, Left zygomatic bone divided into two—"Os Japonicum."	330	112	95	—	63	82	65
NH 48.11.20.5	♀ Complete milk dentition	266	107	86	88	59	71	64
NH 67.12 4.2	♂ ,, ,, ,,	334	104	91	—	58	84	74
Z 2	♂ ,, ,, ,,	315	110	93	—	59	78	66
RCS 14	♂ ,, ,, ,, 1st molar about to erupt.	270	107	87·5	—	58·3	74·4	61·5
NH 47.3.1.5	♂ 1st perm. molar erupting. Basi-occipital fused with exoccipitals.	353	114	94	—	67	81	72
R 3	♂ Milk dent. + 1st perm. molar	—	—	—	—	—	—	70
Z 5	Milk dent. + 1st perm. molar. Occipital in one. Metopic sut. open.	350	115	95	98	68	78	67
RCS 17 *a*	♂ Milk dent. + 1st perm. molar	355	125	96·5	—	62	—	70
CA 13	♀ ,, ,, ,, ,, ,,	315	117	89	—	62	83	71·5
CA 14	♂ ,, ,, ,, ,, ,,	361	116	97	—	69	84	72·5
RCS 17.4	♂ ,, ,, ,, ,, ,,	330	111·5	93·5	—	63	80	66
R 1	♂ ,, ,, ,, ,, ,, Occip. bone in one. Sierra Leone.	—	122	97	101	67	82	72
R 2	♂ Milk dent. + 1st perm. molar. Occip. bone in one.	363	123	94	103	67	88	68
NH 1.8.9.11	♀ Milk dent. + 1st perm. molar	362	125	97	98	64	82·5	71
NH 65.5.9.4	♀ ,, ,, ,, ,, ,,	377	119	96	98	67	84	74
CA 12	♂ ,, ,, ,, ,, ,,	392	118·5	96	—	68	80	73
RCS 13	♀ ,, ,, ,, ,, ,, Perm. med. incisors erupted.	297	119	89	—	59·5	80	65
R 4	♀ Incisors and 2nd perm. molars erupting. Upper Congo.	368	117	98	102	65	84	75
NH 1.8.9.9	♀ Incisors and 2nd perm. molars erupted.	366	126	94	101	64	85	72
CA 11	♀ Perm. incisors and 2nd molars erupted. Premols. erupting.	390	127·5	100	—	67	87	76
R 5	♂ Premolars erupted	351	120	95	108	65	84	74
Z 1	♂ ,, ,,	410	—	—	—	—	—	—
NH 77.8.1.8	Perm. canines erupting	445	130	100	108	64	93	79
RCS 12.5	♀ Complete perm. dentition except for 3rd molars.	300	122	94	—	62	85	63

TABLE I. (*continued*).

No. of Skull.	Description.	Cranial Capacity.	Maximum Ant. Post. Diam.	Max. Transverse Diameter.	Bismatoid Diameter.	Min. Frontal Breadth.	Basion Bregmatic Height.	Auriculo-Bregmatic Height.
NH 87.12.1.1...	♂ Complete perm. dentition except for 3rd molars.	431	131	105	116	73	88	75
RCS 6	♀ Complete perm. dentition except for 3rd molars.	381	135	96	109	68	87	73
RCS 12.51	♂ Complete perm. dentition except for 3rd molars.	382	132	108	—	75	87	67·5
RCS 7	♂ Complete perm. dentition except for 3rd molars. M. 3 erupting in lower jaw.	400	129	101	—	63	85	65
NH 12.10.28.68...	? Complete perm. dentition except for 3rd molars. M. 3 erupting.	375	131	102	119	68	86	71
CA 14 A	♂ Complete perm. dentition except for 3rd molars.	392	138	106	—	66	88	72
RCS 11 A	♂ Complete perm. dentition except for 3rd molars.	415	142	104	—	71	99	70

TABLE I.

Part 2.

Adult Females.

No. of Skull.	Description.			Cranial Capacity.	Maximum Ant. Post. Diam.	Max. Transverse Diameter.	Bimastoid Diameter.	Min. Frontal Breadth.	Basion-Bregmatic Height.	Auriculo-Bregmatic Height.
RCSA 63.4	♀ Adult.	Basi-sphenoid suture open		350	130	98	—	67	84	63
NH 20 4.13.2....	♀ „			350	122	98	117	63	84	66
R 7	♀ „			366	131	97	113	69	86	70
RCS 4	♀ „	Basi-sphenoid just closed. 2nd molar worn.		350	123	94	—	64	88	68
NH 64.12.1.7	♀ „			395	132	99	112	65	93	71
RCS 12.53	♀ „	M. 3 not worn. Cranial sutures still open.	Basi-sphenoid suture fused.	340	130	104	—	64	82	66
R 8	♀ „			455	138	104	127	67	91	74
NH 83.7.28.17 ..	♀ „			362	126	94	105	61	87	70
RCS 17.5	♀ „			365?	129	105	—	73	91	72·5
R 9	♀ „ Gaboon			331	124	94	107	60	81	64
R 13...........	♀ „	All sutures occluded. M. 3 worn.		377	130	97	112	72	89	73
CA 14 *b*	♀ „			370	135	98	—	68	88	73
RCS 6	♀ „			380?	134	—	—	—	91	—
RCS 11 *c*............	♀ „ Deformed vault......			370?	120	97	—	70	—	74
NH 5.4.14.2	♀ „ Liberia			—	129	98	122	63	85	67
NH 5.4.14.1	♀ „			—	137	102	130	67	—	73
NH 95.4.1.1	♀ „ Congo			330	128	96	106	67	87	71
NH 7.1.8.8	♀ „ Nigeria			—	128	95	104	66	86	72
NH 61.29.7.14 ...	♀ „			350	127	98	111	66	92	71
NH 1.8.9.84	♀ „ Toro			345	135	94	115	68	88	69
NH 90.6.8.2	♀ „ Cen. Africa			—	136	100	—	67	—	72
R 10	♀ „ Gaboon			357	125	98	109	64	88	73
R 11	♀ „ Tungen			380	131	100	112	65	87	70
P 1	♀ „			444	137	101	123	66	87	68
R 12	♀ „			290	117	93	107	—	83	67
NH 88.7.28.18 ...	♀ „ Kooloe Kamba			370	130	94	116	65	92	71
R 14..................	♀ „	All teeth very worn		335	130	98	115	62	87	66
NH 87.12.2.1	♀ „ Liberia			384	129	96	115	64	88	69
RCS 2	♀ „			412	137	100	—	66	91·5	66
CA 14 C	♀ „			361	141	101	—	72	87	68
RCS 11	♀ „			357	141	96	—	68	90	69

Table I.

Part 3.

Adult Males.

No. of Skull.	Description.			Cranial Capacity.	Maximum Ant. Post. Diam.	Max. Transverse Diameter.	Bimastoid Diameter.	Min. Frontal Breadth.	Basion-Bregmatic Height.	Auriculo-Bregmatic Height.
R 15	♂ Adult. West Africa.	Basi-sphenoid and other sutures open. M.3 untouched.		370	127	95	117	64	86	67
R 16	♂ „			330	127	96	117	65	87	71
R 25	♂ „ Cameroons.			—	—	117	—	78	—	81
NH 5.4.14.3	♂ „ Liberia.			—	—	—	—	68	90	75
NH 94.7.25.2	♂ „			400	131	99	123	66	84	71
NH 94.7.25.3	♂ „ Bonn.	Cran. sut. open.	Basi-sphenoid suture closed.	460?	141	103	—	65	90	77
R 18	♂ „ Kooloe Kamba.			375	136	100	121	71	92	71
R 17	♂ „ West Afr. M.3 unerupt.	M.3 not worn.		356	129	96	121	68	87	68
RCS 11.2	♂ „ S. Nigeria			455	139	107	—	71	90	65
RCS 11.5	♂ „ Sierra Leone			394	131	104	—	67	81·5	68
RCS 3.	♂ „			380	136	103	—	69	85	64
RCS 12.52	♂ „ Supernumerary peg-like molar			430	135	—	—	70	92	72
RCS 10.5	♂ „	All sutures occluded. M.3 worn.		330	127	94	—	62	87	63
RCS 9	♂ „ Gold Coast			437	143	107	—	63	92	68
RCS 8	♂ „ W. Coast Afr.			415	140	98	—	61	92	68
RCS 10	♂ „ Gaboon			400	133	97	—	62	91	64·5
NH 12.10.28.70	♂ „ S. Nigeria			385	133	102	115	67	90	69
NH 22.12.19.1	♂ „ Belgian Congo			472	138	105	123	67	92	73
NH 64.12.1.6	♂ „			350	129	100	117	66	88	72
R 19	♂ „ Cameroons			415	142	97	127	70	92	79
R 20	♂ „ French Congo			325	135	98	123	67	88	68
R 21	♂ „			425	133	102	126	69	95	76
NH 90.6.8.1	♂ „ L. Albert Nyanza			410	137	105	130	63	88	72
R 22	♂ „ Kooloe Kamba			350	126	96	115	63	79	64
NH 12.10.28.69	♂ „ S. Nigeria			400?	136	99	118	64	92	71
NH 23.1.2.4.1	♂ „ Sierra Leone			410	133	106	127	67	95	78
NH 1.8.9.10	♂ „ Toru			415	135	98	118	65	90	74
NH 61.7.29.10	♂ „			435	139	103	124	70	92	74
NH 17.12.16.1	♂ „			—	133	102	122	65	88	72
NH 23.3.1.1	♂ „ Congo			—	126	97	117	67	82	66
NH 94.7.25.1	♂ „			—	134	—	—	—	90	—
RCS 10.52	♂ „ Sierra Leone			407	131	98	—	63	94	69
NH 2c	♂ „	All teeth v. worn.		—	134	103	125	70	—	74
NH 7.7.8.19	♂ „			410	141	102	122	70	91	76
NH 20.10.21.4	♂ „ Ruanda			350	125	94	113	65	90	67
NH 7.1.8.9	♂ „ S. Nigeria			—	126	102	120	70	84	67
R 23	♂ „ Gaboon			411	138	105	132	69	90	74
R 24	♂ „ Congo			500	145	109	129	72	91	74
NH 82.9.18.1	♂ „			391	133	105	135	67	91	—
RCS 1	♂ „ Gaboon. Peg-like M.4.			403	134	100	—	66	95	71
RCS 12	♂ „ Two peg-like M.4			385	140	108	—	65	88	67

3. The Exterior of the Cranium.

Harris (1926) remarks, regarding the comparison of anthropoid with human skulls, that "all external measurements of length in the anthropoid skull are vitiated by the strongly-developed crista occipitalis, and, in the Gorilla, the more strongly-developed crista supraorbitalis. A fact which has not been so clearly recognized is the still greater error in determining the breadth of the brain-case. The parietal eminences of the anthropoids are not well developed; they do not overlie the point of maximum breadth."

For several reasons, however, it is wise in the study of the growth of the Chimpanzee endocranium not to neglect external measurements. Firstly, the overgrowth of bone, which is such a feature in the development of the temporal and occipital areas of the Gorilla skull, and which leads to the formation of sagittal and occipital crests, is much less marked. The primitive function of the cranium as a brain-case is not so hidden by overgrowth of bone for the attachment of the muscles of the rapidly-growing jaws as it is in the other apes. Occipital crests, never very massive, are formed, particularly in the male, by the fusion of the upwardly-extending nuchal line with the backwardly-receding temporal lines; but the fusion of the sagittal lines, to form a sagittal crest, is a rare phenomenon. In the forty adult males which I examined, it occurred only four times.

The transverse diameter offers all the difficulties that Harris mentions. But if it is possible to obtain a measure of this diameter in all skulls at some point on the cranium not completely masked by overgrowth of bone, then such a diameter should be taken. Fortunately, in the Chimpanzee, the mastoid air-cells do not invade the squamous temporal above the level of the petrous bone. And although it was difficult always to be sure that the points of the calipers were on the same points in each skull, I took a diameter on the lowest part of the temporal squama just before it merges with the mastoid projection—the level of the upper surface of the petrous bone. Selenka and Oppenheim measured higher up on the cranium.

The minimum frontal breadth (see p. 6) was taken in a region where there is no increase in the thickness of bone during growth, and thus variations in this external measurement reflect variations in the interior of the skull.

Similarly, all measurements of height are valuable, for the thickness of bone in the region of the sagittal suture varies very little in old and young skulls; such measurements can, therefore, be employed as an index of variations in the height of the endocranium—except, of course, in the four cases where the sagittal crest developed. I frequently noticed a small depression over the bregma in the old skulls.

A striking instance of the small use one can make of external measurements in estimating the cranial capacity is afforded by skulls R. 15 and R. 16. The external diameters of R. 16 are either identical with, or a millimetre or two larger than, those of R. 15, and yet its capacity is 40 c.c. less. (See Table I. pt. 3.)

External Measurements of Cranium.

a. *Length.*

	Male.			Female.		
	No. of Cases.	Av.	Range of Variation.	No. of Cases.	Av.	Range of Variation.
During milk dent.	7	107	100–112	5	106	99·5–112
With 1st molar	7	119	111–125	5	119	117–125
With 2nd molar and premolars	2	125	120–130	3	123·5	117–127·5
With canines, without M. 3	6	134	129–142	2	128·5	122–135
Adults	39	134	125–145	31	130	117–141

No growth occurs in length after the eruption of the 3rd molar. Apparently the eruption of the canines marks the end point of the muscular development of the jaws. It is interesting to see in this cessation of growth a process attendant on the fact that the third molars in the Chimpanzee, as in Man, are degenerating.

b. *Transverse Diameter* *.

	Male.			Female.		
	No. of Cases.	Av.	Range of Variation.	No. of Cases.	Av.	Range of Variation.
During milk dent.	5	91	87·5–94	5	90	86–92
With 1st molar	7	95	93–97	4	93	89–97
With 2nd molar and premolars	2	98	95–100	3	97	94–100
With canines, without M. 3	6	104	101–108	2	95	94–96
Adult	38	101	94–117	30	98	93–105

Here, too, we find no appreciable increase after the period when the incisors, premolars, and canines erupt; this, however, does not bear so directly upon the regression of the masticatory apparatus as does the lack of increase in the length of the skull;

---

* Owing to an oversight the bimastoid diameter was only measured on the skulls at the Natural History Museum including the Rothschild collection. Until the first permanent molar has erupted, the widest transverse diameter is always found on the brain-box proper.

for in taking this particular transverse diameter the aim was to escape those areas of bone specially developed for muscular attachment. The major part of the 5 or 6 millimetre growth after the eruption of the first molar is due to increased thickness of bone. We shall return to this point in a consideration of endrocranial casts. There are not enough data to demonstrate the increase in the bimastoid diameter after the eruption of the canines. But the few figures collected for these immature stages do not suggest that the growth of this diameter differs much from that of the length of the brain-box—*i. e.*, little growth occurs after the eruption of the 3rd molar.

c. *Minimum Frontal Breadth.*

This diameter is of definite value in estimating variations in the interior of the skull, as there is no appreciable thickening of bone—barely a millimetre or two, if anything—during the whole process of growth at the points where these measurements were taken.

	MALE.			FEMALE.		
	No. of Cases.	Av.	Range of Variation.	No. of Cases.	Av.	Range of Variation.
During milk dent.	7	60	57–64	5	60	57–63
With 1st perm. molar.	7	66	62–69	5	64	60–67
Intermed. stages.........	2	64·5	64–65	3	65	64–67
With canines, without M. 3	6	69	63–75	2	65	62–68
Adults	40	67	61–78	29	66	60–73

Very little growth takes place in this diameter after the first permanent molar has erupted.

d. *Basi-Bregmatic Height.*

	MALE.			FEMALE.		
	No. of Cases.	Av.	Range of Variation.	No. of Cases.	Av.	Range of Variation.
During milk dent.... ..	7	78	73–84	5	78	71–87
With 1st perm. molar .	6	82·5	80–88	5	81	82·5–84
Intermed. stages...... ...	2	88·5	84–93	3	85	84–87
With canines, without M. 3	6	89	85–99	2	86	85–87
Adults	39	89	79–95	28	87·5	81–93

An average increase of 6·5 mm. is shown in this diameter in both sexes after the eruption of the first molar; as has been previously noted, there is no increase in the thickness of the bone itself. Therefore the 6·5 mm is a definite increase in the height of the endocranial cavity.

e. *Auriculo-Bregmatic Height.*

	MALE.			FEMALE.		
	No. of Cases.	Av.	Range of Variation.	No. of Cases.	Av.	Range of Variation.
During milk dent. ..	7	69	61·5–74	5	68	64–74
With 1st molar .	8	70·5	66–73	5	70	65-74
Intermed. stages	2	76·5	74–79	3	74	72–76
With canines, without M. 3	6	70	65–75	2	68	63–73
Adults	39	71	63–81	30	69·5	63–74

The averages obtained for the "Intermediate stages" will not be considered, as they are based on only five specimens. Excluding this group, we find that there is no growth in the Auriculo-Bregmatic diameter after the first molar erupts—not even in the thickness of bone. Seeing that the total height of the endocranial cavity does increase after the eruption of the first molar (basi-bregmatic diameter), the growth in height must take place below the subcerebral plane—in the cerebellum and temporal lobes. This conclusion is similar to the one I arrived at in regard to *Papio porcarius* (1926).

4. CRANIAL CAPACITY.

TABLE II.

An Analysis of the Cranial Capacities in Table I.

	Irrespective of Sex.			Female.			Male.		
Description.	No. of Skulls.	Average cranial capacity.	Range.	No. of Skulls.	Average cranial capacity.	Range.	No. of Skulls.	Average cranial capacity.	Range.
Milk dentition.	**11**	**314 c.c.**	**266–350**	**5**	**309 c.c.**	**266–340**	**6**	**317 c.c.**	**270–350**
Milk dentition + 1st perm. molar.	**10**	**355·8 c.c.**	**315–392**	**4**	**351 c.c.**	**315–377**	**6**	**359 c.c.**	**330–392**
Intermediate stages.	**7**	**357·2 c.c.**	**297–445**	**4**	**355 c.c.**	**297–390**	**3**	**402 c.c.**	**351–445**
3rd molar unerupted.	**8**	**384·5 c.c.**	**300–431**	**2**	**340·5 c.c.**	**300–381**	**6**	**399 c.c.**	**375–431**
Adults.	**61**	**384·5 c.c.**	**290–500**	**27**	**365·8 c.c.**	**290–455**	**34**	**399·5 c.c.**	**325–500**

TABLE III.

Cranial Capacities—Collected Results of Former Observers.

Observer and Method.	ADULT ♂.			ADULT ♀.			SUBADULT SKULLS.				
	No. of Cases.	Av. Capac.	Range.	No. of Cases.	Av.	Range.	No. of Cases.	Age.	Sex.	Av.	Range.
TOPINARD, 1894. Shot.	7	421	382–482	3	404	387–425	1	Milk dent.	?	328	—
VOGT (Topinard, 1894). Millet?	3	—	390–410	—	—	—	—	—	—	—	—
WYMAN (Topinard, 1894). Millet?	7	Sex and age? Range 294–424.									
BISCHOFF, 1867. Method?	1	410	—	5	367	330–460	2	?	?	312	330–324
KEITH, 1895. Collected data. Methods?											
Owen.	1	452	—	3	393	360–436	1	Milk dent.	?	328	—
Turner.	1	360	—	1	393	—	1	?	♀	344	—
Du Chaillu.	4	Sex and age? Average 335·5. Range 262–409.									
SELENKA, 1898. Shot and millet seed. Some collected data included.	24	420	350–480	26	390	320–450	4	Pre-milk.	♀ & ♂	245	220–290
							5	Milk.	♂	352	305–394
							7	Milk.	♀	326	300–350
							12	Milk.	♂ & ♀	336·5	300–394
							5	Milk + M.1.	♂	369	325–422
							3	Milk + M.1.	♀	346	330–364
							8	Milk + M.1.	♂ & ♀	360	325–422
							2	Inter. stages.	♂	390	350–430
							2	Inter. stages.	♀	375	330–420
							4	Inter. stages.	♂ & ♀	382	330–430
OPPENHEIM, 1911. Millet seed.	—	404·3	350–470	—	388·8	350–440	2	Pre-milk.	?	210	140–280
							8	As late as int. stages.	?	—	300–350
HAGEDOORN, 1924. Millet?	6	386·7	340–445	Sex?			3	Milk.	?	268	215–315
							6	Milk + M.1.	?	326	280–285
							2	Inter. stages.	?	355	350–360
Collected data.	106?	411	350–480	106?	385	320–480	1	M3. unerupt.	?	385	
HRDLIČKA, 1925, & MARTIN, 1914.	—	—	350–470	—	—	350–440	—	—	—	—	—

Six of the twenty-seven adult female capacities given in Table I. part 2 are below 350 c.c. and of these, five lie between 330 c.c. and 350 c.c. R 12, with a capacity of 290 c.c., is probably an example of a microcephalic Chimpanzee skull. The lowest normal capacity is in the region of 330 c.c. Similarly, a capacity below 350 c.c. is rare amongst males, only three occurring in the series of 34, Table I. part 3, two with a capacity of 330 c.c. and one with that of 325 c.c. Nineteen (56 per cent.) have capacities above 400 c.c. The mean capacities I obtained for adults are lower than those of previous observers. Selenka's figures are 20 c.c. higher than mine *. Bearing this in mind, a glance will show that his curves for adults are practically the same as mine (text-figs. 1 and 2).

Sexual differentiation in cranial capacity is not marked in the early stages (see Table II.). It commences to develop after the eruption of the first permanent molar. The average difference between the adult male and female is 34 c.c. (Selenka found 31 c.c.; Oppenheim 15·5 c.c.; Hagedoorn, from collected data, 26 c.c.; and Topinard 17 c.c.) If the adult male capacity is reckoned as 100, then the adult female is 91·5. (Selenka 93, Oppenheim 96, Hagedoorn 93·5, Topinard 96.) My figures have, however, been obtained from a larger series than those of previous workers.

The average capacity, irrespective of sex, for the stage of Milk Dentition + 1st Molar is 13·3 per cent. higher than that during Milk Dentition. In males the increase is 13·2 per cent.; in females 13 6 per cent.

The average capacity for adults, irrespective of sex, is 8·1 per cent. higher than for individuals of the stage "Milk Dentition + 1st Molar." In males the increase is 11·3 per cent.; in females 3 per cent.

The average capacity for adults, irrespective of sex, is 2·5 per cent. greater than the capacity during the intermediate stages.

The average capacity for the group of eight (irrespective of sex), with only the third molar of the permanent dentition unerupted is the same as for adults. There are only two females in this stage, and it is to be expected on the score of numbers that their average capacity should differ from that of the adult females, as it does; but it is surprising to see that the six males have an average capacity the same as that of the fully adult males.

Unfortunately, on account of the paucity of material belonging to the "Intermediate Stages" and the "Third Molar Unerupted" groups, it is impossible to state whether or not there

---

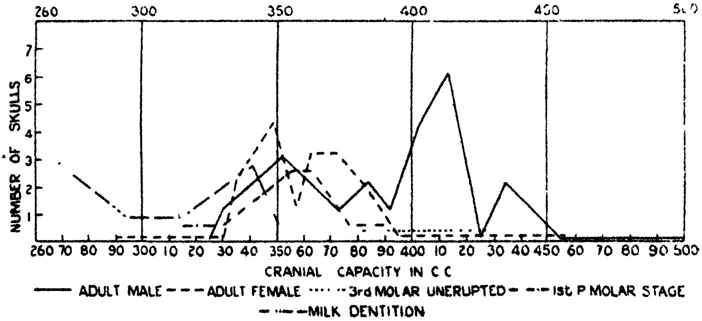
* A 5 per cent. difference between millet seed and shot estimation is large. Nevertheless, there is a consistent variation between Selenka's determinations and my own for adults which make our results comparable. In the subadults there is no constant difference. It must be remembered that Selenka used shot, millet seed, and peas for his estimations. In his descriptions it is not clear whether he used all three in each skull, or whether he varied the procedure from one to the other.

is a period between the eruption of the first permanent molar and maturity when brain-growth abruptly ceases. The few figures that we have for these stages do not suggest any such phenomenon.

An examination of the range of capacity in the different stages also merits consideration. (See Table I.) 36·5 per cent. of the milk dentition skulls have capacities below 300 c.c.; none has a capacity above 350 c.c., which is, practically speaking, the lower limit for adults.

Of the next group—those with the first permanent molar erupted—only one skull has a capacity less than 300 c.c., but none again exceeds 400 c.c. Seven of the ten have capacities between 350 c.c. and 400 c.c. A considerable amount of growth must occur between the eruption of the last milk tooth and that of the first permanent tooth.

Text-figure 1.



59 per cent. of the 34 adult males have capacities above 400 c.c.—one has a capacity of 500 c.c. Only three, or 11 per cent., of the adult females exceed 400 c.c. One can see that, particularly in the male, growth must continue for a long while after the eruption of the first permanent molar.

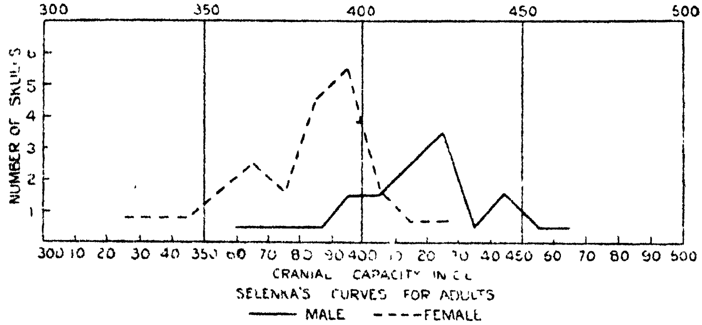
The range of capacity in the "Intermediate Stages" and "Third Molar Unerupted" groups is not so large as in adults.

Selenka alone of previous observers has met with capacities in the early stages which exceed my limits. He records three male skulls of milk dentition with capacities of 394 c.c., 375 c.c., and 370 c.c. respectively, and one male, in which the first permanent molar had erupted, that had a capacity of 422 c.c. Allowing for the different technique in capacity estimation, the skull with a capacity of 394 c.c. alone does not accommodate itself to the limit of capacity I found for its stage. The other three would most probably approach the limits I have found, for Selenka's method, as I have mentioned previously, gives values some 20 c.c. higher than mine.

Text-fig. 1 consists of curves from the various stages superimposed one on another. The extension in range of capacity with the onset of each stage is well marked. Text-fig. 2 is a copy of Selenka's curves for his adult Chimpanzees.

There is no evidence for Oppenheim's suggestion that growth in capacity ceases when the sutures occlude. All the evidence suggests a possible continuation of growth until the stage preceding the eruption of the third molar, but there is no evidence as yet for any growth after that period.

Text-figure 2.



Assuming the adult capacity to be 100, the capacities of the earlier stages according to various observers are as follows:—

Observer and No. of Skulls.	Irrespective of Sex.		Male.		Female.	
	At Milk Dentition.	After Eruption of 1st molar.	At Milk Dentition.	After Eruption of 1st molar.	At Milk Dentition.	After Eruption of 1st molar.
Present investigation, 82 skulls.	81·7	92·5	79·4	89·9	84·5	96
Selenka, 70 skulls.	83·2	89	84	88	84	88·7
Hagedoorn, 15 skulls.	69·3	84·3	—	—	—	—

Keith, from his collected data (1895), estimated that the capacity at the end of the "Milk Dentition + first permanent Molar" stage was 90 per cent. of the adult capacity. Selenka stated that after the eruption of the second permanent molar the capacity was 94–97 per cent. of the adult size. He had

only four skulls, however, for this stage. The average capacity for my seven skulls of the "Intermediate" stage is 97·5 per cent. of the adult.

5. ENDOCRANIAL CASTS.

We come now to a more accurate method of determining the form and variations of the endocranial cavity—namely, by means of casts. Unfortunately this, although the ideal method of undertaking a study of the brain-box, has its limitations: one, the amount of labour entailed in obtaining an accurate cast; and another and more important one, the fact that few museum authorities approve the idea of sectioning specimen skulls.

Moreover, an objection is frequently lodged against the method on the score of inaccuracy. It is said that the sawcut removes 1 mm. or 1·5 mm. band of bone as sawdust (Harris, 1926), and thus reduces the breadth or height of the cranium, depending on the line the sawcut takes, and so reduces the capacity. Actually this is not always the rule. As Wingate Todd has pointed out (1923), there are sometimes one or two places which the saw has not severed and which break when the two portions of the skull are separated, leaving irregular joints which fit together accurately when the two halves are opposed. In this way a crack, the width of which corresponds to the amount of bone removed, separates the two parts of the skull. About three of the twelve skulls from which casts were taken had been sectioned badly, and the divided portions did not fit together accurately; only one, however, was markedly bad. All but four of the twelve skulls had been sectioned by former observers. N.H. 82.9.18.1. is a cast belonging to the Natural History Museum. (Table I. part 3, & Table IV.)

Wingate Todd mentions a further objection to casts as a means of obtaining accurate figures for the cranial capacity—namely, that plaster when wet increases in volume. This objection has been overcome in the past by Wagner, who weighed the cast, and by Welcker, who varnished the plaster and then estimated the volume.

It is necessary, therefore, to indicate my procedure. The plaster casts were made in the usual manner from gelatine casts of the interior. After they had been thoroughly dried, they were placed in liquid stearine, and allowed to remain until the stearine had displaced all the air in the pores of the plaster—generally about half an hour. They were then removed and wiped dry. It is found that no stearine adheres to the surface, and the plaster, when cut, has a peculiar solid consistency all its own. Water has no effect on its volume when it is treated in this way.

The cast volumes were obtained by water-displacement—measuring the overflow which escapes through a tap soldered into the side of a round tin, the diameter of which was just larger than the greatest diameter of the casts. The procedure is simple: the tap having been closed and a wire "cradle" placed inside, the tin is filled with water; as soon as the water-level is steady the tap is opened; water then escapes until the level of the water reaches the lowest point of the opening of the tap into the tin; the tap is then closed again and the cast immersed gently on the cradle; the tap is not opened to let out the overflow until the oscillations in the water-level cease. By employing this method carefully the same reading for a cast can be obtained time after time.

TABLE IV.

Endocranial Casts.

Number of Skull.	Cranial capacity with shot.	Volume of Endocranial casts.	Volume minus Cerebellar portion.	Volume of Cerebellar portion.	Maximum Ant. Post. Diameter.	Maximum Transverse Diameter.	Basi-Bregmatic Height.	Height above Subcerebral plane.	Height above Temporal lobes.	Width of Cerebellum.	Index Encephalicus.
RCS 17. M.D., ♀ . .	270	272	248	24	95	83	68	52	67	70	87
CA 14 *d*. M.D., ♂ .	295	295	267·5	27·5	88·5	83	71	51	73	72	84
RCS 14. M.D., ♂ .	270	273	247	26	99	84·5	70	49	67	80	85
CA 13. M.1, ♀ .. .	315	311	267·5	43·5	104	83	73	51	67	74	80
RCS 12.5. M. 3 absent, ♀ ..	300	290	249	41	101	82·5	78	48	69	75·5	81
RCS 4 A. Cran. sutures open, ♀	350	343	299	44	105	88	82	52	75	78	84
CA 14 *c* A. Aged ♀ ..	361	356	324	32	114·5	89	79	50	71	81	78
RCS 3 A. Middle age ♂	380	370	310	60	113	94	78	50	72	85·5	83
RCS 10.5 A. M. 3 worn, ♂	330	322·5	269	53·5	102	87	78	51	74	80	85
RCS 9 A. M. 3 worn, ♂ ..	437	420	379	41	115	95	83	55	76·5	80	83
RCS 8 A. M. 3 worn, ♂	415	400	348	52	115	91	85	56	75	80	79
NH 82.9.18.1. A ♂	—	391	334·5	56·5	108·5	93	86	54	76·5	84	86

The casts vary greatly in form. No two can be said to resemble each other closely in detail. A very close correspondence in general appearance is found in an Orang (cast from skull R.C.S. 49, Milk Dentition and first permanent Molar) and the Chimpanzee R.C.S. 4. But while the parietal region in the Orang is better developed than that of the Chimpanzee, the reverse occurs in the frontal. (See Pls. I., II., and III.)

It is impossible to remove from the cast the exact amount which must have constituted the volume of endocranium beneath the tentorium cerebelli. To obtain the volume of the cast, minus what is called the cerebellar portion, the following procedure was employed:—The portion of cast below the middle of the transverse sinus was chipped away to leave in each case a flat surface which led up to the pituitary fossa. In all cases, at the region where the transverse becomes the sigmoid sinus, it was necessary to chip below the sinus in order that the exposed surface should be perfectly flat. The portion removed does not represent half the cerebellar endocranium, for it is quite possible for the cerebellum to extend upwards in one case more than in another; neither does it represent the endocranial volume below the subcerebral plane. However, a means is thus provided of comparing a portion of the cerebellar endocranium in one cast with the same portion in another.

The variations in the form of the cerebellar endocranium were strikingly demonstrated when taking the maximum antero-posterior diameter of the cast of R.C.S. 10.5, when it was found that the posterior arm of the calipers had to rest on the cerebellum —an instance where the cerebrum did not completely cover the cerebellum. Occasionally a slight asymmetry is found in the cerebral hemispheres. In R.C.S. 4, R.C.S. 8, and C.A. 13 the left occipital lobe is larger than the right. In C.A. 14 the right is the larger.

The value of the water-displacement volumes of the casts as a control to the figures obtained for the cranial capacities with shot was demonstrated on p. 6. It was shown that the average error by shot was 2·2 per cent., the average absolute error being 7 c.c. The shot-values are generally too high. The average volume of the adult casts is 1·19 times the average volume of the casts belonging to the stages of "milk dentition" and "milk dentition plus first molar." The volume of the adult cast minus the "cerebellar portion" is 1·26 times the volume of the corresponding part during these early stages. The adult cerebellar portion is 1·6 times the volume of this portion during the early stages. It is clear, therefore, that after milk dentition a greater amount of growth takes place below than above the subcerebral plane.

As far as linear dimensions are concerned, Table IV. shows that there is an increase in length of 1·25 cm. after milk dentition. The length of the cast of the first molar stage is 0·5 cm. more than the average length of the milk-dentition group. The transverse diameter increases after the early stages 0·5 cm. in the female and 0·8 cm. in the male.

The height-measurements are interesting; they demonstrate growth after milk dentition in the total height of the endocranium, but not in the height above the subcerebral plane. Thus the basi-bregmatic diameter increases after the two early stages, 1 cm. in the male and slightly less in the female; whereas no growth in the height above the subcerebral plane occurs after milk dentition. The same conclusion was reached in considering the external basi-bregmatic and auriculo-bregmatic diameter.

The height from the lower surface of the temporal lobes to the vertex increases in both sexes about 0·5 cm. after the first molar erupts. The width of the cerebellum increases by about 0·5–0·8 cm.

During milk dentition, before the mastoid region develops, the cephalic indices, exocranial and endocranial, are alike. The exocranial index varies, of course, with the development of the mastoid and occipital regions, but there is no change during growth in the index encephalicus (Bolk, 1925; Harris, 1926), which varies in all stages from 79–87. It is interesting to note that the most brachycephalic (index encephalicus) of the twelve skulls occurs among the three of milk dentition, and the least brachycephalic is the adult female.

Text-fig. 3 *a* has been constructed by superimposing outline drawings of the norma verticalis of four casts—an adult of each sex, one from the three of milk dentition, and the sole representative of the resting stage after the eruption of the first molar. The casts chosen were those whose volumes were nearest the average capacity of their groups.

In text-fig. 3 *b* the same casts are used and profile drawings are superimposed, using the basion as a fixed point and letting the points where the temporal lobe meets the orbital surface in profile fall on the same line.

General Summing-up of the Growth of the Endocranial Cavity.

The capacity of the skull in the male during milk dentition is 80 per cent., and during the resting stage following the eruption of the first molar 90 per cent., of the adult capacity. In the female these two values are 85 and 95 per cent. respectively.

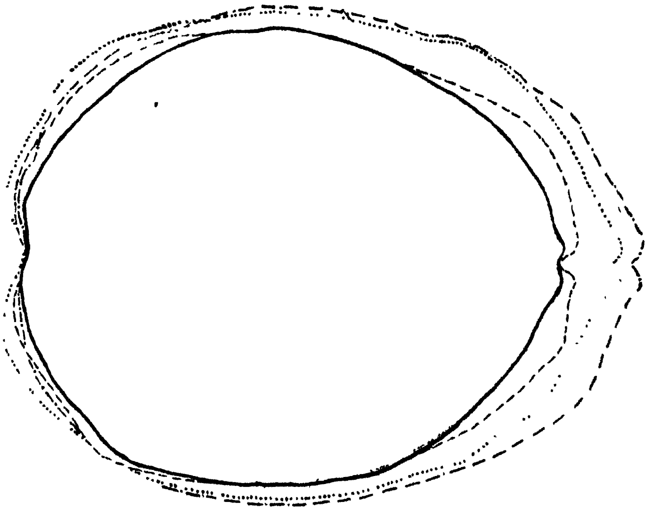
Sexual differentiation commences to manifest itself markedly after the eruption of the first molar, and in adults the average female capacity is 91 per cent. of the average male.

There is evidence for continuation of growth into the resting stage preceding the eruption of the third molar. The growth in the endocranial cavity manifests itself in all directions, but more particularly below the subcerebral plane.

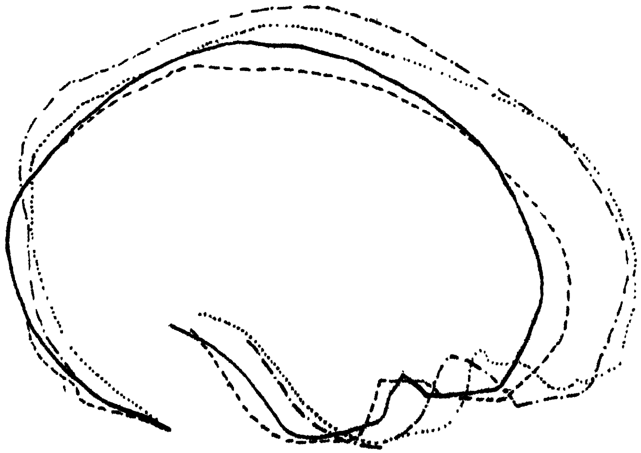
6. Eruption of the Teeth.

Broderip was the first to record the age of a Chimpanzee (1835). He writes of an animal, said to be one year old, living at the Zoological Society's Gardens, in which all the deciduous teeth had erupted. Ehlers (1881) gives a record of a Chimpanzee whose teeth were erupting between the ages of six and twelve. The greater part of the known data in regard to tooth-eruption has been collected by Sir Arthur Keith. In 1895 he gave the ages of five animals, but recorded the stage of dentition in only

Text-figures 3 *a* & 3 *b*.



A.



B.

one, Sally, mentioned again in 1899. This animal died when ten years old, and her canines and second and third molars had not then erupted. Johanna, another ape mentioned in 1899, had lived twelve years in captivity, and at the end of this period her third molars had not completely cut the gums. It is stated, on the strength of an observation of her keepers, that six years before this she possessed her first permanent molars and all her incisors. Sir Arthur very kindly placed at my disposal a comparative table of tooth-eruption which he drew up about twenty-five years ago. In this the milk teeth are said to erupt before the middle of the second year. The period of eruption of the permanent teeth is placed at from four to twelve years in the Chimpanzee, five to thirteen years in the Orang, and six to twenty-one in Man.

Yerkes (1925) writes of the Chimpanzee as follows:—"Milk teeth begin to appear in the first or second month, and before the end of the first year all have been acquired. It is Madame Abreu's belief, based on repeated observation, that the Chimpanzee usually begins to lose its milk teeth in the fifth and sixth years, and that these are replaced by permanent teeth by the age of seven or eight. The change, she says, is very rapid, occupying only a few weeks, or at most a few months."

These observations of Madame Abreu are in such contradiction to all others, including those I have recently made at the Zoological Gardens, that they will not be considered here. But one or two remarks in Yerkes's book with regard to Chimpanzee age are of interest. He states that most Chimpanzees exported from Africa are more than two years old, and the majority are from three to five He also considers that the Chimpanzee probably lives as long as Man, and that its life-stages are very little different, except that puberty is reached some two or three years earlier. Madame Abreu made some interesting observations regarding the weaning and menstruation of animals born on her estate. She noted that the Chimpanzee is weaned at nineteen months, and that menstruation commences between eight and ten years of age. With regard to the latter, her evidence is substantiated by Ehlers.

My own observations were made on the five Chimpanzees now living at the Zoological Society's Gardens. One of these, a female named Boo-Boo (donated August 27th, 1927), is a newcomer from the Gold Coast. When examined on September 28th, 1927, she was found to possess a complete temporary set of teeth, and, in addition, the first permanent molars fully erupted in the lower jaw and almost through in the upper. Of the others, Jimmy, a male from West Africa, has been in the Gardens since December 14th, 1923—almost four years. When examined in November, 1926, he was in possession of a complete temporary set of teeth plus the first permanent molars which had just cut. When examined on September 28th, 1927, no alteration in his dentition was found to have occurred in the intervening ten months. Jack, a male from the Gold Coast, has been in the Gardens since July 25th, 1926. In November, 1926, his mouth was examined, and he was found to possess the first permanent molars, upper and lower permanent central incisors, lower lateral permanent incisors erupting, with, in addition, the milk canines and one milk molar. I examined him a second time, on September 28th, 1927. In the intervening period of ten months the milk molar had fallen out, the lower lateral incisors had fully erupted, and both premolars in the right upper jaw had erupted. Other premolars were just commencing to erupt. Peculiarly enough, the upper lateral incisors had not yet erupted. Such an irregularity in dentition did not occur in any of the Chimpanzee skulls I examined, and I have not seen it recorded in the anthropoid literature*.

The fourth animal is Clarence, a male from the Belgian Congo, who arrived at the Gardens on March 2nd, 1926. The head of this animal, as well as that of the next, has been X-rayed on three occasions for Dr. John Beattie, until recently Anatomist to the Zoological Society, by Mr. F. Melville, radiographer at University College. These radiograms were taken at six months' intervals, commencing on the 30th May, 1926.

In the first picture it is seen that Clarence has a complete temporary set of teeth. The roots of the first permanent molars are not calcified, though the alveolar margin has been absorbed, and the crowns of the teeth are level with the alveolar margin; calcification is present in all the permanent teeth except the third molar, but only very slightly in the second molar and canines. In the second radiogram the first permanent molar has fully erupted. In the third the condition is the same, except that the dental sac of the third molar is visible: calcification has proceeded fairly rapidly in the other teeth. When the animal itself was examined in November, 1926, the first molars were cutting the gums. Since then no change in his mouth has occurred.

---

* The usual order of appearance of the teeth in the Chimpanzee, judging from the series of skulls examined, is as follows:—(1) First permanent molars. (2) Medial incisors. (3) Lateral incisors. (4) Second molars. (5) First premolars. (6) Second premolars. (7) Canines. (8) Third molars. Selenka, from his series, determined the same sequence, with the one exception that the lower second molar erupted before the lateral incisor. The skull on which he based this statement must have been irregular in the order of appearance of its teeth, just as Jack's, to my mind, is abnormal. In both Jack and Sally the premolars erupted previous to the eruption of the second molars.

Such irregularities in the sequence of eruption (though seldom recorded in the literature) are common in Man. The usual order differs from the Chimpanzee's in that the premolars and canines erupt before the second molars. In Tomes's 'Dental Anatomy' (1923) it is mentioned that certain authors consider that the canines erupt before the second premolars.

The times of eruption as recorded in text-books vary greatly. The tendency in some works is to extend the period of eruption. Thus, in Quain's 'Anatomy,' the second premolars are said to erupt at twelve years, whereas in others (Cunningham, Gray, Morris, Piersol, etc.) the second premolar is said to erupt at ten. Morris gives both premolars erupting together between the ages of nine and ten, while Livy (quoted by Piersol) found in the majority of children he examined that the lateral incisors and both premolars erupted in the tenth year.

I have examined the mouths of fifty-three children between the ages of five and nine. Surprising irregularities in the sequence of eruption were encountered. In five the medial incisors were erupting before all the first permanent molars had appeared. One child, aged 7 7/12 years, showed a stage of dentition almost similar to that of the Chimpanzee, Jack. The first permanent molars were fully erupted. All four lower and the upper medial incisors were through, while both upper left premolars had erupted; the first upper right premolar was just cutting the gum.

The times of appearance of the teeth were, if anything, early. In all but one of eighteen children older than seven, the first permanent molars were in place; in the one exception, a child aged 7 2/12 years, only two had erupted. In seven of sixteen children younger than six, first permanent molars had erupted. Premolars had erupted in four of five children older than eight, and in one child younger than ight.

Bi-Bi, the last animal, is a female from Nigeria, who came to the Gardens on April 21st, 1926. Previous to that she had been the donor's pet for one year. The first radiogram of this Chimpanzee, taken on the 30th May, 1926, is practically identical with the first one of Clarence, except that there is no absorption of bone over the first permanent molar. The picture taken six months later shows this in progress, and corresponds more closely with the first one taken of Clarence. The roots of the first molar have not yet calcified. The picture taken early in June, 1927, shows the crowns of the first molars above the alveolar margin, those of the lower jaw in advance of those of the upper. Calcification has proceeded apace in the other teeth, but there is no sign of the third molar. When the animal itself was examined in November, 1926, she was found to possess a complete temporary set of teeth. When examined in September, 1927, the first permanent molars were found to be through in the lower jaw and just commencing to cut the gums in the upper jaw.

An analysis of these facts, as I shall proceed to show, has led to the interesting conclusion that the period of eruption of the permanent teeth in the Chimpanzee is practically the same as in Man. We may be perfectly certain that the age of an animal like the Chimpanzee is not likely to be over-estimated; the danger lies in under-estimation. *Sally's* (1895) *age at death, computed from her years of captivity, was ten*: which means that she could not have been younger than ten. *Her stage of dentition corresponds with that of a child of ten.*

Johanna supplies rather doubtful information. Six years previous to the eruption of her third molars her keeper had noticed her permanent incisors, but he did not note her other teeth. It is quite likely that her premolars and second molars had erupted; if they had not, then the period of eruption of these teeth and canines would have been surprisingly short compared with the resting stage following the eruption of the first molar. Granting the animal two years of freedom before she entered on her life of captivity (the low limit set by Yerkes), her third molars then erupted at the age of fourteen. For various reasons mentioned below I consider this a very low estimate.

Jimmy, after he had been three years at the Zoological Gardens, cut his first permanent molars. If, again, we accept Yerkes's estimate that apes brought from Africa are more than two years old*, *then Jimmy cut his first molars at the age of five or six, which is the age at which this tooth erupts in a child.*

The eruption of the teeth is not a continuous process, but it is interrupted by resting stages. In the Human an interval of four years follows the eruption of the milk teeth, after which approximately one year intervenes between the eruption of the various teeth, until another long interval of at least five years separates the third molar from the second molar and canines. Two resting stages have been observed in the Chimpanzee. *Since the eruption of Jimmy's first molar, a year ago, no change has taken place in his dentition. Clarence cut his first molars about a year ago, and he, too, does not appear to be in imminent danger of losing his milk incisors. This stage occupies a year in Man* †.

The change which has taken place in Jack's mouth during the observed period of ten months is no more than has occurred in a similar period in a child now aged 7 7/12 months (see footnote to p. 24). The sequence of eruption in this child was abnormal, but *a similar change could have occurred in any child during any period of ten months between the ages of eight and ten.* Sally (1895) died at ten years of age with no more than the first molars, incisors, and premolars of the permanent dentition erupted. Judging, therefore, from her, the premolars erupt at nine or ten years of age. The Sally (1928) mentioned in the footnote on page 26 was also about this age when her premolars appeared. The lateral incisors, accordingly, erupt about eight or nine. When Johanna's (1895) teeth were first noted, all her incisors were in place. She must have been, therefore, at least nine years of age. Six years after this, that is when she was fifteen years old, her third molars erupted.

---

* The fact that Madam Abreu had noted that Chimpanzees are weaned at nineteen months lends colour to this view. It is very doubtful if an unweaned Chimpanzee could be transported alive from Tropical Africa into the rigours of a Northern climate. The keepers at the Zoological Gardens have informed me that they have never had to exercise any special care with the diet of the younger and smaller animals, such as would be expected if they were unweaned.

† An examination of thirty radiograms of the heads of children taken about the time the first molar erupts has convinced me that the speed of eruption is no greater in Man than it is in the Chimpanzee. These children were all hospital patients. In only one were radiograms taken at six successive intervals between the ages of 5 1/12 and 6 1/12 years; as in the Chimpanzee, the interval between the appearance of the tooth at the alveolar margin and when fully in place was about six months.

The five Chimpanzees at the Zoological Society's Gardens were re-examined on the 25th October, 1927. No apparent change has taken place in the mouths of Boo-Boo, Bee-Bee, and Clarence during the previous month. Jimmy's medial incisors were very loose; this may be due in part to the severe pyorrhœa and gum recession from which he, in common with almost all the others, suffers, but the physical signs indicated that his permanent central incisors would cut shortly. During the previous month the crowns of Jack's right lower second premolar and left upper first premolar have pierced the gums.

Clarence died in December, 1927. Unfortunately, I have not, as yet, had an opportunity of examining his remains. An examination of the other Chimpanzees on the 6th February, 1928, revealed the following:—No apparent change had occurred in Bee-Bee or Boo-Boo. Jimmy's permanent lower median incisors were appearing through the gum, though his milk incisors had not fallen out. The duration of the resting stage following the eruption of the first molar was in his case, therefore, fourteen months. In Jack, all the right premolars were in place. The lower left premolars, the upper lateral incisors, and the lower left second molar were just appearing through the gum. The upper left premolars were not quite in place. Another animal, a female named Sally, was examined for the first time on this date. She had been three years in the Gardens, and was said to have been seven years old on arrival. She commenced menstruating at eight; she was found to have all her first molars, incisors, and premolars. Her lower second molars were in place, her upper seconds had just pierced the gum. For ten years of age, she was therefore slightly in advance of the Sally mentioned by Sir Arthur Keith in 1895.

There is certainly no functional need for an early appearance of the third molar in the Chimpanzee. It has long been recognized that the Chimpanzee dentition resembles the human more than it does that of any ape, and that the third molar is degenerate. Indeed, in one fully adult male skull, R 17, Table I. part 3, in which all the sutures were occluded, they had not erupted, and there was no sign of them. In addition, the condition of the third molar, as I have pointed out, influences the general growth of the skull, and this influence is shown in the lack of overgrowth of bone for muscular attachment, such as occurs in the cranium of the Gorilla after the eruption of the canines and third molars*.

The fact that the number of skulls in our collection with only the third molar unerupted (9) is larger than the number for all the intermediate stages together (7), is also suggestive of a lengthy period between the eruption of the canines and the third molars. In any large collection of immature skulls the number found at each stage will depend upon the duration of that stage and upon the death-rate, granted that the birth-rate remains steady. Thus in Man, assuming the death-rate during milk dentition to be the same as in the period when the first permanent molar alone has erupted, one would expect to find—since the former period is four times as long as the latter—four times as many skulls of milk dentition as skulls with the first permanent molar alone erupted. In our collection of Chimpanzee skulls, accumulations occur at three stages: twelve of milk dentition; twelve with the first molar erupted; and nine with the third molar unerupted. A fair proportion of the skulls of the two earlier stages are the remains of Zoological Gardens specimens, among whom the infant death-rate is high. Practically all the adult and subadult specimens were collected in Africa, and in these the death-rate is never so high as in the very early stages. The presence in our series, then, of more of these subadults than of specimens of all the intermediate stages together indicates that, whether their deaths were natural, or due to human intervention, there were more of them roaming about. If the same proportions were maintained in 160 instead of 16 skulls, one could emphatically state that the last resting stage in the eruption of the teeth occupied as much time as did the eruption of all the other permanent teeth—a state of affairs which prevails in Man. Unfortunately, the series consist of 16, and not 160 specimens, and I can only claim that these results suggest a longer duration for this than for the earlier stages.

---

* In the Gorilla the functional need for the third molar is evidenced by the fact that it generally erupts before the canines. In primitive peoples, too, the third molar is known to erupt early. Professor G. Elliot Smith has informed me that he has seen Copts in Egypt of fifteen years of age with erupted third molars.

The Zoological Gardens specimens, amongst whom, as I have remarked, the infant death-rate is high, form a large proportion of the accumulation of the Milk Dentition and First Molar stage; and this is probably the reason for the relatively large number of specimens of this stage. The period of repose following this eruption may, however, be longer than is suspected. There is definite evidence for a year; the more exact duration will be settled as soon as the Zoological Gardens apes at this stage shed their incisors. (See footnote, p. 26.)

The calcification of the permanent teeth occurs at the same relative times as in Man. In Man, calcification of the second molar commences at five. In the radiogram of Bi–Bi. taken twelve months before the eruption of her first molar, it is seen that calcification of the second is just commencing. Calcification of the third molar commences in Man at nine years. In the last radiogram taken of Clarence, about seven months after the eruption of the first permanent molar, there is no sign of calcification, though a dental sac is just visible. As in Man, calcification in all the other permanent teeth is apparent a year before the eruption of the first molar.

My conclusions are, therefore, that all the available data indicate that the duration of the Chimpanzee stages of tooth-eruption are the same as in Man. The first permanent molar erupts between five and six, and the last molar does not erupt before fifteen, probably later. The other teeth erupt at practically the same time as in Man, with the exception of the second molar, which appears early—as far as is known, always before the canine, and either before or after the premolars.

7. ENDOCRANIAL VOLUME AND BRAIN VOLUME.

Keith (1895) states that " owing to the paucity of observations on the brains of anthropoids, one is compelled to utilise their cranial capacities as a basis from which to calculate their brain-weights. " In Man," he goes on to say, " brain-weight, stated in grammes, is, on the average, equal to 87 per cent. of cranial capacity stated in cubic centimetres ; . . . . . the curious fact is evidenced in the anthropoids that the brain-weight stated in grammes exceeds the cranial capacity expressed in cubic centimetres. Symington found that the cranial capacity of a female Chimpanzee measured 360 c.c., while its brain weighed 368 gms. This observation is independently substantiated by Milne-Edwards, recording in the 'Comptes Rendus de l'Academie de Sciences' that he found the brain of a male Orang to weigh 400 gms., while its cranial capacity amounted to only 365 c.c. ; . . . . . there is no great risk of error in using the cranial capacities of anthropoids as directly indicative of their brain-weights."

Apart from the fact that records of brain-weight are scanty, one should remember that the estimates are usually made under such varied conditions that the results are rarely comparable. This applies particularly to the anthropoids, where no one observer has measured more than about six brains, and where some of the records are those of brains which had been preserved in alcohol, formalin, or saline. The latter records are of little value, as the gain or loss in weight of a brain immersed in these fluids depends on numerous factors not completely understood. and in no two cases is the loss or gain the same.

There are several possible sources of error, even when the brains are weighed shortly after removal from the skull. The chief is probably the loss of weight which occurs due to drainage of the cerebrospinal fluid when the brain is left for longer or shorter intervals after removal. Although the extent of this loss has been accurately determined (Pfister, 1897), it is but rarely taken into account. Again, sometimes the brain is weighed with all its membranes, sometimes without. And, finally, Matiegka (1902) has shown that the condition of the blood-vessels—dilated with blood or constricted according to the cause and manner of death—has a marked influence on brain-weight.

Owing to the absence of reliable data, therefore, it becomes necessary to ascertain variations in brain volume from the variations in endocranial volume. But it has first to be shown that there is a definite relation between the two.

As the function of the cranium is primarily that of a brain-case, it would be expected that the endocranium expands to accommodate an increase in the size of its contents—nervous tissue proper, the membranes, cerebrospinal fluid, and blood-vessels. The development of the last three has been shown to be dependent on the development of the brain. We should expect, therefore, that when brain-growth ceases there is no further change in the size of the endocranium. This has been proved by Pfister (1902), who showed that there was parallel growth in brain and endocranial volume.

Wingate Todd (1923) remarks that "the brain volume plus the volume of cerebrospinal fluid represents the true maximum physiological brain volume. . . . . . Of course it is impossible to ascertain how fully the brain ever occupies the total possible space at its disposal. If it is true that the actual brain volume decreases with advancing age, at least after the adult period is reached, it may never fill the possible space in any circumstances. But the actual volume of the brain determined after death is not necessarily more accurate than the maximum possible physiological volume, as an index of brain volume during life."

Moreover, he has made the valuable discovery that, in Man, the amount of decrease in cranial capacity which occurs when a skull passes from the "fresh" to the "bone dry" state is approximately equal to the volume of the dura. It follows, then, that the cranial capacity of a dried skull is the physiological volume of the living brain. There is little doubt that these findings would apply also to the anthropoids; in which case, the values obtained for the Chimpanzee's capacities (Table I.) would be the same as the physiological brain volumes, and the conclusions I arrived at with regard to the growth in capacity would apply equally to growth in physiological brain volume.

It has been suggested that the cranial capacity in both Man and the Anthropoids decreases in the more advanced stages of life (Blakemen, 1905; Keith, 1910); but I have no evidence for such a decrease in the Chimpanzee. Thirty-four skulls of the adult male series in Table I. have had their cranial capacities estimated, and of these the seventeen older specimens have capacities 6 c.c. larger, on the average, than the younger seventeen. Of the twenty-seven adult females whose cranial capacities were measured (Table I.), the older thirteen have capacities 5 c.c. less, on the average, than the younger thirteen. These results are probably due to chance, and one suspects that in a series ten times larger the older half would have average cranial capacities identical with those of the younger.

Rudolph (1914) also denies that there is any thickening of the vault bones in old age, causing a decrease in cranial capacity *pari passu* with the decrease in brain volume.

But even if the cranial capacity remains constant after it has attained full size, it is nevertheless true that the brain volume decreases. Fortunately, a great deal of research has been carried out on this subject.

Donaldson (1895) states that "the relations of the brains to the cranial cavity vary with age, sex, and cause of death. The brain appears more nearly to fill the cranial cavity in the young than in the adult; in old age there is an increasing diminution in both weight and volume."

Rudolph (1914) corroborates this statement. The difference between brain volume and the capacity of the fresh skull with dura intact is 2½ per cent. in new-born children, and in children from one week to six years old 3 per cent. This amount increases until the end of puberty to an average of 7½ per cent., varying from 5 to 10 per cent. These figures are maintained, he states, until middle age—68 in the male, 58 in the female, and there is no sexual difference. He attributes the observation of Bischoff (1880) that the female brain fills the endocranium by 3 to 4 per cent. more than the male, to the fact that Bischoff obtained the result from observations on too small a series of skulls.

Rudolph cannot establish the onset of cerebral atrophy with certainty on account of inadequate data, but he is certain that between middle age and extreme old age the 7½ per cent. difference between brain volume and the cranial capacity with dura intact increases to 15 per cent.; *i. e.*, a decrease in brain volume of 15·6 per cent. occurs. He points out that there are great individual differences in the time of onset. It must be noted that he did not work with the dried skull; all his results apply only to material worked on shortly after death. They can, however, be adjusted according to the values for skull shrinkage given by Wingate Todd.

Rudolph gives the average dura volume as 50–60 c.c., or 3½ per cent. of the capacity of freshly-macerated skull, and he is unable to find any sexual or age difference. Larger skulls have a proportionately larger volume of dura. The capacity of the sinuses is about 50-60 c.c. He gives three very interesting observations on dogs, amongst whom brain volume varies from 70–90 c.c. The difference between the brain volume and cranial cavity with the dura intact is between 1 and 2 per cent.; without dura, about 5 per cent. This indicates that small brains fill the endocranial volume at their disposal more than do large brains. If the capacity of the fresh human skull with dura intact is reckoned as 100, the capacity of the fresh macerated skull (without the dura) is 107. The brain volume in adults is 92·5. By multiplying the volume of the brain by the specific gravity it is possible to get the brain-weight. Thus obtained, brain-weight expressed in grammes is 10–11 per cent. less than the fresh cranial capacity expressed in cubic centimetres.

Bolk's material (1904) indicated that the specific gravity of the brain varies with age. In the newly-born it is under 1·030, and it reaches the average adult figure 1·034 when about six months old. There is no sexual variation, but it varies with the cause of death.

Rudolph criticised Bolk's work on the relation of brain volume to cranial capacity on the grounds that, firstly, the brains were measured three days after death, during which time they had swelled by absorption of water; and, secondly, his skulls were measured when they were neither completely dried nor in a fresh wet state. Bolk's results are, nevertheless, interesting. The smaller the brain the nearer is its volume to the cranial capacity. The percentage relationship varies between 97 and 81. Until the fiftieth year in the male it keeps above 93 per cent.; after that it falls fairly rapidly, and between 80 and 90 is as low as 86 per cent. Senile atrophy commences at the same time in both sexes.

Pfister (1903), working on infants and children, concluded that the dura reaches adult proportions about the third year. He estimated that the volume of the freshly-macerated skull (apparently in the same condition as Rudolph's) could be obtained from the volume with dura intact by adding 6½–7 per cent. This is the same value that Rudolph estimated.

Estimations of the date of onset of cerebral atrophy in Man vary from author to author. Matiegka (1902) places it about sixty in the male and fifty in the female. According to

Marchand's (1902) numerous data, the commencement of diminution in volume occurs at eighty in the male and seventy in the female.

Raymond Pearl (1905) believes that "there is a steady decline in the weight of the brain with advancing age, beginning at about the twentieth year and continuing throughout adult life." In arriving at this conclusion he used the figures provided by Marchand, Bischoff, Retzius, and Matiegka. Cerebral atrophy begins, according to Donaldson (1895), at fifty-five in the male and forty-five in the female. He states that the actual date of onset varies a great deal from individual to individual. Handmann (1906) places it at sixty, while in Pape and Kopelsky's tables (1926) diminution in brain-weight begins at fifty. As one reason for this statistical phenomenon, the latter authors suggest that since so many people with heavy brains die young, cerebral atrophy is generally exaggerated.

If no diminution in cranial capacity occurs, compensating changes must take place in the volume of dura, in other membranes, or in the volume of cerebrospinal fluid to make up for this loss in volume of the brain.

Wingate Todd (1923) writes: "By comparing Pffister's figures for dura volume in the child with our own, it is apparent that there is little or no increase in dura in volume after infancy; . . . . age, at least in adult life, has no bearing on the dura volume. Sex and stock have no influence either." These observations are followed up in 1923 with further work on the dura, in which he was able to show that there is "a small increase in dura volume with advancing age, and also that there is a small proportional increase corresponding to size of cranium."

Anderson (1910) found that the dura volume remains constant, occupying 4·5–5 per cent. of the cranial cavity. Wingate Todd (1923) accounts for this discrepancy between his results and Anderson's as probably due to weakness in technique on the latter's part. But Anderson's statement, "It is also apparent that the fluid varies inversely with the brain volume, and it would appear as if the diminution of the brain volume is compensated by an increased amount of cerebrospinal fluid," is the first definite reference I have found to a compensatory process which to-day is recognized as the reaction of all the skull-contents to shrinkage in brain volume. There is no necessity for postulating a decrease in the cranial capacity in adult age. This has been proved by Stillman (1911), who made a thorough study of pial and cerebral œdema in a very large number of cases. From an examination of the literature and of his own data, he comes to the conclusion that the onset of brain atrophy varies from individual to individual, and that the varied times of onset mentioned in the literature are due to this. But, whatever the time of onset, "the collection of fluid in the pia mater is not *per se* a pathological process, but in every instance represents the reciprocal of brain shrinkage." Thickening of the pia as age advanced was first noted, however, by Broca (quoted by Topinard), who also made out a sexual difference. So, too, Greenfield and Carmichael (1925) give one of the functions of the cerebrospinal fluid as "filling up the cranial cavity when the bulk of the brain shrinks from disease or senility."

It is thoroughly established, then, that, in Man, the endocranial cavity continues to increase as long as the brain increases. When, however, brain atrophy sets in, compensatory increase in volume occurs in the membranes and cerebrospinal fluid, and there is, therefore, no need to assume any decrease in cranial capacity.

We have no evidence of cerebral atrophy in the Chimpanzee, but if it does occur, the absence of decreased capacity in aged skulls suggests that the same process operates as in Man.

8. THE CONTRAST BETWEEN HUMAN AND ANTHROPOID BRAIN-GROWTH.

At this stage it would be interesting to discover whether the ape's brain differs much in its growth from the human. Although there are numerous data regarding the latter in the literature, there are unfortunately few series of figures which provide brain-weights for both adults and children.

It has always been recognized that the greater part of brain-growth occurs early in life. According to Pfister, a third of the total growth is achieved by the end of eight months, and the second third by the end of two and a half years; the final third is added very gradually, cessation of growth occurring at about twenty years of age. Marchand's results were similar. The brain doubles in weight in nine months, and is trebled at the end of the third year. From that point, growth is very slow, cessation occurring in about the twenty-first year; the increase in the female is less than in the male. The average brain-weights of new-born children, in Marchand's series, were 371 gms. for the male and 361 gms. for the female. Pfister does not give average weights for new-born infants.

The cessation of growth may occur at any time until twenty-one, the age at which the third molar generally erupts, if it erupts at all. Though this is the general conclusion, there are some who would extend this period further. Sims, quoted by Marchand, would go as far as the forties: this is an extreme view, however. Bischoff (1880) extends the limit well into the twenties; while Venn (1890) and Galton (1890) consider that the heads of University men continue to grow after twenty.

Donaldson, from a consideration of Vierodt's figures, comes to the conclusion that by the seventh year the encephalon has reached approximately its full weight. In Vierodt's series the maximum weight is reached between the ages of thirteen and fifteen in both sexes; but such a result is not the rule.

If the adult Chimpanzee capacity is reckoned as 100, then the capacity during milk dentition in the male is 80, in the female

85. The capacity in the resting stage after the eruption of the first molar is 90 in the male, 95 in the female.

Below are similar estimations for Man from the brain-weight data in the literature. The four years between the second and sixth birthdays were considered to represent milk dentition, and the year between the sixth and seventh the first molar stage.

Observer.	Milk Dentition.		First Molar.	
	♂.	♀.	♂.	♀.
Boyd (Marchand)	80	85	—	—
Marchand	89	90	100	100
Handmann	88	90	98	100
Vierodt (Donaldson)	89	91	96	100

The values for the seventh year are surprisingly high in view of the fact that both Handmann and Marchand estimate that brain-growth does not cease until the twentieth year. Boyd's data alone provides percentages for the early stages similar to those I found in the Chimpanzee. It appears as though the results drawn from our study of the cranial capacity have flattered the Chimpanzee with regard to the amount of brain-growth that occurs after milk dentition. At the same time it must be remembered that the results obtained by this treatment of the Human brain-weight figures do not correspond to the conclusions of their respective authors.

Handmann, for instance, finds the new-born brain-weight to be 400 gms. in the male. According to his conclusions, this, by the fourth to the sixth year, will increase to 1200 gms. The adult weight is 1370 gms., so that 170 gms. are still to be added after the eruption of the first molar. Nevertheless, the average weight for the seventh year in his series is the same as the average adult weight. It appears, therefore, that the high results for this year are chance ones, due to the fact that rather higher weights than normal cropped up in the tables, in which data for the seventh year form a very small proportion.

Marchand, Handmann, and Vierodt, however, arrive at remarkably similar values for the proportions of the brain-weight during milk dentition to the weight of the adult brain. It is due, perhaps, to the fact that all three drew their data from the least-favoured classes of society.

The later brain-growth in the Chimpanzee occurs chiefly in the cerebellum. According to Pfister, the Human brain during post-natal development increases until it is nearly four times its original size. The cerebellum, however, grows until it is seven times its size at birth. The cerebellar growth, too, is much more rapid than that of the cerebrum, and by the end of the first six months one-third of its total growth has occurred. The second third is added by the end of the second year, while the final third is not completed until about the twenty-first year.

Reichert found that the proportion of cerebellum to cerebrum is smaller in large brains, and larger in small brains. The

Chimpanzee brain in this respect may be considered a small brain. Whereas the proportion of cerebellum to the whole brain is normally about 10–11 per cent. in Man, the few estimations that have been made of this ratio in the Chimpanzee (Moller, 1891) are in the neighbourhood of 14 per cent. It may be assumed, therefore, that in the Chimpanzee the cerebellum plays a greater part in influencing total brain-growth than it does in Man.

According to Marchand, sexual differentiation in brain-weight is well marked in Man at four years. A graph made from Vierordt's data (Donaldson) shows that there is no sexual differentiation until six months, at which age the male brain becomes on an average 50 gms. heavier than the female. This difference in brain-weight remains much the same until seven years, when it increases to about 150 gms. This is maintained throughout life, except at one period, the fifteenth year, when the female brain-weight is found, statistically, to exceed the male. Our series of Chimpanzee skulls did not show marked sexual differentiation until after the eruption of the first molar—that is, in the sixth year.

On the whole a comparison of Human with Anthropoid brain-growth is not justified, chiefly because of the small amount of Anthropoid data. As far as it is possible to tell, a relatively greater amount of growth occurs in the Anthropoid. But it would not be surprising to discover, with more data, that the same growth-process occurred in each.

9. The Taungs Ape.

Elliot Smith, in the second edition of his 'Essays on the Evolution of Man' (1927), made use of my findings regarding the growth of the endocranial cavity in estimating the possible growth in the Taungs ape. I shall briefly reconsider the problem, since the inclusion of new skulls has altered my average values.

It is the considered opinion of most authorities that *Australopithecus* is a form of ape which fits easily into the Simian family, though all consider that certain refinements and infantile traits elevate it slightly above the other members of its family. Dart (1926), Broom (1925), and Sollas (1925) believe that a separate family should be created between the anthropoid apes and *Pithecanthropus* for its inclusion.

There is, however, no reason to assume a growth-process in the new South African ape different from that which operates in the Chimpanzee. The first permanent molar had just appeared previous to its death. The age was therefore estimated at four years in view of former theories of anthropoid growth. I have indicated, however, that the available data establish the time of eruption of the first molar in the Chimpanzee as during the sixth or seventh years. It is accepted that times of tooth eruption are the same throughout the anthropoids. *Australopithecus* must, therefore, have been one to two years older than was formerly estimated.

The endocranial volume, according to Dart, is 520 c.c. He allowed for a further expansion of 20 per cent., arriving at an adult capacity of 625 c.c. Keith placed the volume at 450 c.c. and allowed 15 per cent. for expansion, the adult volume becoming 520 c.c. My own estimate of the capacity as obtained from a reconstructed endocranial cast, presented to University College by Professor Dart, is 500 c.c. By analogy with the Chimpanzee, subsequent growth will vary with sex. The average expansion, regardless of sex, after the eruption of the first molar is 8·1 per cent. In the male, the average expansion is 11·3 per cent.; in the female, 3 per cent. The final capacities would therefore be:—regardless of sex, 540 c.c.; male, 566 c.c.; female, 515 c.c. The expansion thus allowed, although far smaller than the arbitrary estimates of Dart and Keith, is liberal compared with that which would occur in a similarly aged human being. Elliot Smith has drawn attention to the very small cerebellum of the Taungs ape. It is here, as he suggested, that most of the later brain-growth might have occurred.

Hrdlička and Robinson have suggested that the Taungs ape was a female. Experience of Chimpanzee skulls of similar age leads me to believe that sex cannot be determined in the absence of numerous specimens in the same stage of dentition; even then, it cannot be decided with certainty.

It must, however, be remembered that brain-growth can cease entirely during milk dentition. In the Chimpanzee series (Table I.), for instance, while the lowest capacities for animals of the age of the Taungs ape are 315 c.c. in a female and 330 c.c. in a male, the capacities in certain adults are as low as 290 c.c. in a female and 325 c.c. in a male. Even if the endocranial volume of the Taungs ape were the lowest that an animal of its age and kind could have, one would find among a large series of specimens capacities as low in the adult. But it is very improbable that *Australopithecus* does possess the lowest possible capacity for its age; one would therefore except to find even lower capacities amongst adults of its kind.

If we assume that the cranial capacity of the Taungs ape is the lowest possible at its age, then, arguing from Chimpanzee analogy and assuming that it could expand and reach the adult maximum, it would undergo a growth, if male, of 54 per cent.; if female, of 57 per cent.: in the first case its final volume would be 769 c.c.; in the second 785 c.c. But it is obviously ridiculous to expect any one skull, in the development following the eruption of the first molar, to go through an amount of growth equal to the entire range of capacity from the infant minimum to the adult maximum. *It is certain, therefore, that 785 c.c. is far above the upper limit of capacity.*

If, on the other hand, we assume its cranial capacity to be the largest that an animal of its age and kind could have, it would already border on the average capacity for adults. To reach the maximum capacity it could continue to grow 27·5 per cent. if male, 21 per cent. if female, the final volumes being 638 c.c. (male) or 603 c.c. (female).

Arguing, therefore, on Chimpanzee analogy, it would be *theoretically* possible for the endocranial volume of an adult *Australopithecus* to vary from under 500 c.c. to 785 c.c. Had the particular ape discovered by Professor Dart lived until it was fully adult, it is extremely unlikely, however, that *its* cranial capacity would have exceeded 550 c.c.

Hagedoorn found the cranial capacities in 27 adult male Gorillas to vary from 450 to 655 c.c., with an average of 550·3 cc. By including the data of Selenka and Oppenheim, an unreliable procedure, he raises the number of his series to 99, with capacities ranging from 420 to 655 c.c. and an average of 520 c.c. Harris, more recently (1927), has shown that the range for the Rothschild series of 34 adult Gorilla skulls is from 415 to 652 c.c., with an average of 490 c.c. The males, 27 in number, range from 440 to 652 c.c., with an average of 513 c.c., and the females, 11 in number, from 415 to 470 c.c., with an average of 442 c.c. The hypothetical adult Taungs ape would fit easily into either range, for its capacity in the region of 550 c.c. leaves a margin of over 100 c.c. on either side.

Dart wishes to put the Australopithecoid " range of brain fluctuation within the range for Pithecanthropids." We have estimated an extreme upper limit for cranial capacity in *Australopithecus* at 785 c.c. This figure is, as we have pointed out, ridiculously high, while imagination alone can suggest a range for *Pithecanthropus*. If we are to seek parallels to the probable adult cranial capacity of *Australopithecus* among the other Primates, we have obviously to turn towards the Gorilla.

As far as the exterior of the cranium is concerned, one cannot assume that *Australopithecus* in its growth will necessarily follow the Chimpanzee. The growth of the exterior of the cranium depends chiefly upon the form of the adult jaws. There can be little doubt that the jaws of the Taungs ape are more refined than those of large anthropoids of similar age (see Pl. IV.), but it is questionable whether this refinement would be carried through into adult life.

Beyond their vertical position there is nothing, so far discovered, in the teeth of *Australopithecus* which differentiates them from those of other anthropoids. Broom declares that " the small size of the incisors is a human character "; but he is not taking into account the fact that Gorilla milk incisors may be even smaller than those of the Taungs ape. The Gorilla permanent dentition is about twice as massive as a Chimpanzee's, in spite of the fact that it may have smaller milk incisors. Dart, in his first description, writes that " the tips of the canine teeth transgress very slightly the general margin of the teeth in each jaw ", but Hrdlička, from an examination of the actual fossil, considers that " the milk canines are distinctly larger and higher than the incisors." It is unreliable to draw hard-and-fast conclusions from Professor Dart's excellent plaster cast, and therefore it is difficult, in the face of these conflicting views, to make any statement. I may mention, however, that in the cast the canines in no way differ from those of any of the young anthropoids. The first permanent molars, too, are larger than those of Chimpanzees. Keith states, also from an examination of a cast, that they are only slightly smaller than those of the Gorilla. As this statement has never been questioned by Dart, I take it that this is the condition in the original fossil. One can only conclude, with this indication of the general size of the permanent dentition, that the jaws of *Australopithecus* could not have been less massive than those of the Chimpanzee. It must be remembered, too, that the Chimpanzee dentition is degenerate, and, owing to this, very little overgrowth of bone on the cranium follows the eruption of the canines. It is doubtful if *Australopithecus* in its development would have retained any other infantile characteristic beyond this. For these reasons I consider it justifiable to make a statement regarding the external form of the cranium of the hypothetical adult Taungs.

The maximum antero-posterior diameter of *Australopithecus* is 127 mm., and the estimated maximum transverse width 95 mm. (Hrdlička). The auriculo-bregmatic and basi-bregmatic diameters are, as estimated from the cast, 80 and 95 mm. respectively. Our range of these four diameters in Chimpanzees of *similar* age are from 111 to 125 mm., 89 to 97 mm., 65 to 74 mm., and 80 to 88 mm. respectively. The averages are 119 mm., 95 mm., 70·5 mm., and 82 mm. Except in transverse width, the Taungs' diameters exceed the *average* diameters for Chimpanzees, but in no case by as much as 1 cm. The Taungs' measurements almost fall within the range of Chimpanzee variation. Its adult measurements, allowing it average growth, would have been as follows:—Length 143 mm., transverse width (above the projections due to the mastoid air-cells) 101 mm., basi-bregmatic diameter 103 mm., and auriculo-bregmatic diameter 80 mm In the total height of the cranium alone do these exceed the known variations in adult Chimpanzees.

10. SUMMARY.

1. 112 Chimpanzee skulls were examined; of these 40 were subadult.

2. The average cranial capacity in the adult female is 365·8 c.c., the range being 290–455 c.c. In the male the average capacity is 399·5 c.c., with a range of 325–500 c.c.

3. Sexual differentiation in cranial capacity is not marked until after the eruption of the first permanent molar. In the adult female, endocranial volume is 91·5 per cent. of the adult male.

4. The brain may continue to grow until the resting stage previous to the eruption of the third permanent molar.

5. During milk dentition the average capacity of the male skull increases to 80 per cent., and during the resting stage following the eruption of the first molar to 90 per cent. of the average adult capacity. In the female these two values are 85 per cent. and 95 per cent. respectively.

6. According to these figures, the amount of growth in the cranial cavity after milk dentition and the eruption of the first permanent molar is almost twice as much as would occur in the human skull—for there during milk dentition the capacity is already 90 per cent. of the adult capacity. This result may be due to the paucity of the anthropoid material.

7. Growth in the endocranial cavity manifests itself in all directions, but more particularly below the subcerebral plane.

8. The available data indicate that the durations of the Chimpanzee tooth stages are practically the same as in Man. The first permanent molar erupts between five and six years, and the last molar at fifteen, or later.

9. The Taungs ape must have been in its sixth or seventh year. Its cranial capacity is estimated at 500 c.c., and, working on the basis of Chimpanzee data, its adult endocranial volume, irrespective of sex, would have been 540·5 c.c. If the skull is that of a male, the adult volume would have been 556·5 c.c., and if a female 515 c.c.

10. The possible cranial capacity in an adult *Australopithecus* is estimated to range from under 500 c.c. to 785 c.c. This upper limit is, however, much too high. It is improbable that the adult capacity of the specimen found would have exceeded 550 c.c.

11. The range of capacity in adult male Gorillas (Hagedoorn and Harris) is from 415 c.c. to 655 c.c., which would easily include the probable capacity (550 c.c.) of the adult of the Taungs' specimen.

12. The external measurements of length and breadth of the cranium of *Australopithecus* fall almost within the range of variation of Chimpanzee skulls of similar age. The height-measurements, on the other hand, are above the maximum of the Chimpanzee.

I wish to express my indebtedness to Professor G. Elliot Smith, of the Institute of Anatomy, University College, for his valuable criticism; to Dr. H. A. Harris, Assistant-Professor in the Institute of Anatomy, University College, for his critical examination of my data and for his very helpful advice; to Mr. L. Fatti, University College Hospital, for assisting me in the collection of data regarding tooth-eruption in children; and to Mr. Hancock, the technician of the Anatomical Museum, University College, for his indipensable assistance in the preparation of the endocranial casts.

11. Literature.

Anderson, J. H 1910 The Proportionate Contents of the Skull. J. Roy. Anthrop. Inst. xi.

Anthony, R., & Villemin, F. 1923. Recherches sur le développement du *Papio porcarius.* Paris, Histoire Naturelle, Fasc. 1. Paul Geuthner.

—— & Coupin, F. 1925–1926 Introduction à l'étude du développement pondéral de l'encéphale. Exemplar e Xenius Gorjanovic-Krambergerianis. Zagreb.

Bartlett, A D. 1885. On a Female Chimpanzee now living in the Society's Gardens. Proc. Zool. Soc London.

Bischoff, T. L. W. 1867 Ueber die Verschiedenheit in der Schadelbildung des Gorilla, Chimpansé und Orang outang (Munchen).

—— 1871 On the Chimpanzee Brain. SB. Math. Phys Cl. Ak. Wiss. Munchen

—— 1880. Das Hirngewicht des Menschen (Bonn).

Blakeman, J. 1905 A Study of the Biometric Constants of English Brain-weights, and their relationships to External Physical Measurements. Biometrica

Bolk, L 1904. Beziehungen zwischen Hirnvolum und Schadelcapacitat, nebst Bemerkungen uber das Hirngewicht der Hollander. Petr. Camper, Nederl. Bijdr. tot de Anatom. Bd. ii. p. 511.

Braune, W. 1891 Das Gewichtsverhaltniss der rechter zur linken Hirnhalfte beim Menschen. Arch. f. Anat. u Phys.

Broderip, W T 1835 On the Habits and External Characters of a Chimpanzee Proc Zool. Soc. London

Broom, R 1925. On the Newly-discovered S. African Man Ape. Natural History.

—— 1925 Some Notes on the Taungs Skull. Nature, cxv. pp. 569–71.

Broomell, I. N., & Fischelis P. 1923 Anatomy and Histology of the Mouth and Teeth. London · Kempton.

Cunningham, D. J 1922 Text-Book of Anatomy Oxford Medical Publications.

Dart, R. A 1925, Feb 7. *Australopithecus africanus.* The Man-Ape of South Africa. Nature.

—— 1925, Sept 26 The Taungs Skull. Nature.

—— 1926. Taungs and its Significance. Natural History, xxvi.

Donaldson, H. H. 1895 The Growth of the Brain. London: Walter Scott, Ltd.

Dubois, E. 1897. Über die Abhangigkeit des Hirngewichtes von der Korpergrösse bei den Saugethieren. Arch. f. Anthrop. xxv.

—— 1898. Über die Abhangigkeit des Hirngewichtes von der Korpergrösse beim Menschen Arch. f. Anthrop. xxv.

Du Chaillu, P. B 1861 Characters of Chimpanzees. Proc. Bost. Soc.

Duckworth, W. L. H. Studies in Anthropology Cambridge Univ. Press.

—— 1915. Morphology and Anthropology. Second Edition, vol. i. Cambridge University Press.

Ehlers, P. 1881 Beitrage zur Kenntniss des Gorilla und Schimpanse. Abh. Phys Cl Ges Wiss. Gottingen.

Elliot Smith, G. 1925, Feb. 14. The Fossil Anthropoid Ape from Taungs. Nature.

—— 1927. Essays on the Evolution of Man. Oxford Univ. Press.

Flower, W. H. 1882. Acrocephalic Skull of a Chimpanzee. Proc. Zool. Soc. London.

Gray, H. 1926. Anatomy. London: Longmans, Green, & Co.

Greenfield, J. G., & Carmichael, E. A. 1925. The Cerebrospinal Fluid in Clinical Diagnosis. London: Macmillan & Co.

Gregory, W. K. 1922. The Origin and Evolution of the Human Dentition. Baltimore. Williams & Wilkins.

Hagedoorn, A. 1924 Schadelcapaciteit van Anthropomorphen. Ned. Tydschr. v. Geneesk

Handmann, E 1906 Über das Hirngewicht des Menschen. Arch f Anat. u. Phys.

Harris, H A 1926. Endocranial Form of Gorilla Skulls. Am. J Phys. Anthrop.

——— 1927. The Skull, the Face, and the Teeth of Primates, with special reference to Dolichocephaly and the Centres of Growth in the Face.—Part I Proc. Zool. Soc. London, pp 191-502

Hartmann, R. 1885. Anthropoid Apes London. Kegan Paul, Trench & Co

Hrdlička, A 1905. Brain-weight in Vertebrates Smithson. Misc. Coll. xlviii

——— 1925. The Taungs Ape Am. J. Phys. Anthrop viii.

——— 1925 Weight of the Brain and of the Internal Organs in American Monkeys, with data on Brain-weight in other Apes. Am. J. Phys. Anthrop viii

Keith, A. 1895 The Growth of Brain in Men and Monkeys. J. Anat. & Phys xxix

——— 1896 Introduction to the Study of the Anthropoid Apes. Natural Science

——— 1899. On the Chimpanzees and their Relation to the Gorilla. Proc. Zool Soc. London

——— 1910. Description of a new Craniometer and Certain Age-changes in the Anthropoid Skull J Anat. & Phys xliv.

——— 1925, Feb 14 The Fossil Anthropoid Ape from Taungs

——— 1925, Feb 14. The New Missing Link. Br. Med. J

——— 1925, July 11. The Taungs Skull Nature.

——— 1925, Sept. 26. The Taungs Ape Nature.

Kohler, W. 1925 The Mentality of Apes. Translated by Ella Winter. London: Kegan Paul, Trench, Trubner & Co.

Lapicque, L. 1908. Tableau genéral des poids somatique et encéphalique dans les especes animales Bull. Soc Anthrop Paris.

Macnamara, N. C. 1902 Craniology of the Primates. Rep. Smithson. Inst

Marchand, F. 1902. Ueber das Hirngewicht des Menschen. Nr. iv. des xxvii. Bds. d. Abhandlg d. Mathem.-physik. Kl. d Kgl. Sachs. Gesellsch d. Wissenschaften.

Marshall, J. 1892 On the Relations between the Weight of the Brain and its Parts, and the Stature and Mass of the Body in Man. J. Anat. & Phys. xxvi.

Martin, R. 1914. Lehrbuch der Anthropologie. Jena.

Matiegka, H. 1902. Ueber das Hirngewicht, die Schadelkapacitat, und die Kopfform. I. Über das Hirngewicht des Menschen. SB. d Kgl. bohm Ges d Wiss.

Moller, J. 1891. Beiträge zur Kenntniss des Anthropoiden-Gehirns. Abh. d. K. Zoolog. u. Anthrop. Mus. zu Dresden.

Morris, H. 1907. Human Anatomy. London Churchill.

Oppenheim, S. 1911. Zur Typologie des Primaten Craniums. Z. f. Morph. & Anthrop. xiv.

Pape, —, & Kopelsky, — 1926. Lancet, No. 5373.

Pearl, R. 1905. Some Results of a Study of Variation and Correlation in Brain-weight. L. Comp. Neurol. & Psych. xv.

——— 1905. Biometrical Studies on Man. I. Variation and Correlation in Brain-weight. Biometrika, iv.

Piersol, G. A. 1907. Human Anatomy. Philadelphia: Lippincott.

Pffister, H. 1897. Das Hirngewicht im Kindsalter. Arch. f. Kinderheilkunde, xxiii.

——— 1903. Die Kapazität des Schadels beim Säugling und alteren Kinde. Monatsschr. f. Psych. u. Neurol.

Pffister, H. 1903. Ueber das Gewicht des Gehirns und einzelner Hirnteile beim Säugling und älteren Kinde. Neurol. Zentralbl. Nr. 12.

Quain, J. 1923. Anatomy. London: Longmans, Green & Co.

Ranke, J. 1896. Vergleichung des Rauminhaltes der Rückgrat und Schädel-Höhle. Bastian-Festshcrift.

Reichardt, M. 1906. Über das Gewicht des menschlichen Kleinhirnes im gesunden und kranken Zustande. All. Z. f. Psych. u. psych.-gericht. Med.

Robinson, A. 1925, March 21. The Taungs Skull. Brit. Med. J.

Rudolph, O. 1914. Untersuchungen über Hirngewicht, Hirnvolumen und Schadelkapazitat. Beit. z. path. Anat. u. z. all. Path. lviii.

Schultz, A. H. 1924. Growth-Studies on Primates. Am. J. Phys. Anthrop. vii.

Selenka, E. 1896. Die Rassen und der Zahnwechsel des Orang-Utan. SB. Math. Phys. Cl. Ak. Wiss. Berlin.

——— 1898–1900. Studien uber Entwickelungsgeschichte der Tiere. Zweiter, Band i. & ii. Menschenaffen.

Sollas, W. J. 1925, June 13. The Taungs Skull. Nature.

——— 1925. Sagittal Section of *Australopithecus*. Quart. J. Geol. Soc. lxxxii. pt. 1.

Sonntag, C. F. 1923. The Anatomy, Physiology, and Pathology of the Chimpanzee. Proc. Zool. Soc. London.

——— 1924. The Morphology and Evolution of the Apes and Man. London: John Bale Sons & Danielson.

Spitzka, E. A. 1903. Brain-weights of Animals, with special Reference to the Weight of the Brain in the Macaque Monkey. J. Comp. Neurol. xiii,

Stillman, C. K. 1911. Edema of the Pia-Arachnoid. Arch. Internal Medicine, vol. viii.

Thompson, D'A. W. 1917. On Growth and Form. Camb. Univ. Press.

Tomes, C. S. 1923. Manual of Dental Anatomy. London: Churchill.

Topinard, P. 1878. Anthropology. London: Chapman & Hall.

Venn, J., & Galton, F. 1890. Cambridge Anthropometry. Nature.

Villiger, E. 1925. Brain and Spinal Cord. Ed. W. H. F. Addison. Philadelphia and London: J. B. Lippincott Company.

Virchow, L. 1880–1882. Gorilla Skulls. SB. der Kön. K. Akad. Berlin.

Weber, M. 1896. Vorstudien uber das Hirngewicht der Säugethiere. Festschrift f. Carl. Gegenbaur.

Weigner, K. 1903. Ein Beitrag zur Bedeutung des Gehirngewichts beim Menschen. Anat. Heft. lxxi. Göttingen.

——— 1906. Kurze Bemerkung zur Herrn E. Handmanns 'Ueber das Hirngewicht des Menschen.' Arch. f. Anat. u. Phys.

Wingate Todd, T. 1923. Cranial Capacity and Linear Dimensions in White and Negro. Am. J. Phys. Anthrop. vi.

——— 1923. Dura Volume in the Male White Skull. Anat. Rec.

Yerkes, R. M. 1925. Almost Human. London: Jonathan Cape.

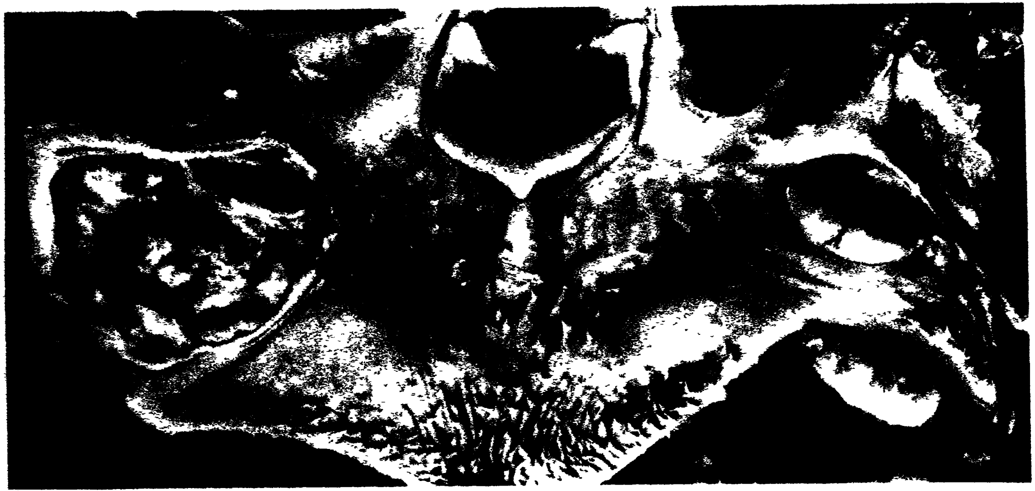
Zuckerman, S. 1926. Growth-changes in the Skull of the Baboon, *Papio porcarius*. Proc. Zool. Soc. London.

EXPLANATION OF THE PLATES.

Plate I. the Normæ Verticales, Plate II. the normæ Laterales, and Plate III. the Normæ Occipitales of Anthropoid Endocranial Casts. From left to right, and from above downwards, they are:—(1) R.C.S. 4; (2) R.C.S. 49; (3) Gorilla; (4) R.C.S. 17; (5) C.A. 14 *d*; (6) C.A. 13; (7) R.C.S. 12.5; (8) C.A. 14 *c*; (9) R.C.S. 3; (10) R.C.S. 10.5; (11) R.C.S. 9; (12) R.C.S. 8; (13) N.H. 82.9.18.1.

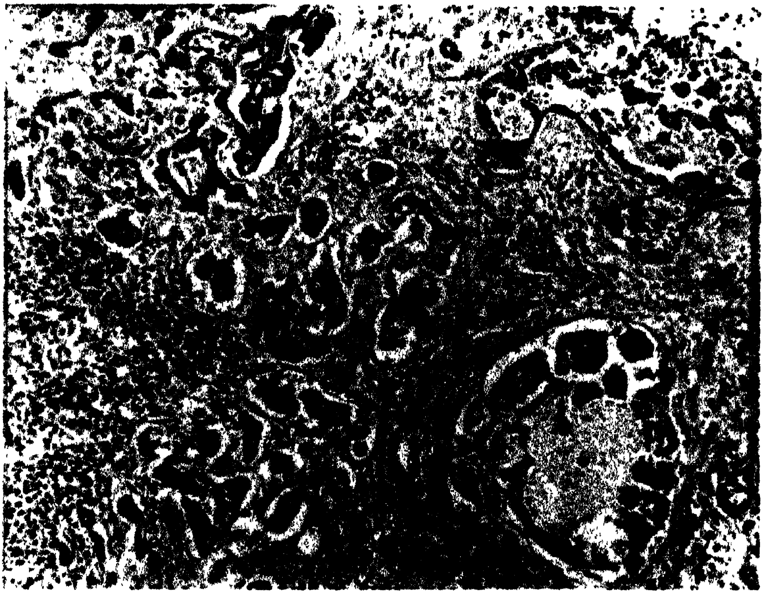
R.C.S. 49 is the Endocranial Cast of an Orang skull of the Milk Dentition and 1st Molar Stage. The Gorilla Endocranial Cast is that of an adult male. The rest are Endocranial Casts from Chimpanzee skulls (Table IV.).

Plate IV. Photographs of a cast of the fossil Taungs Ape, and of a Chimpanzee skull of similar age. Photographs by F. Melville.

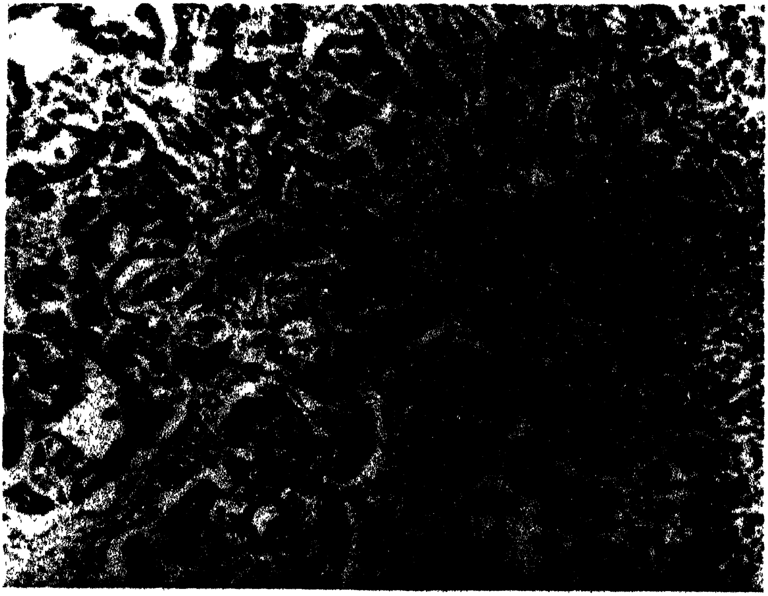


1

Carcinoma of Tonsil in a Common Wolf (*Canis lupus*)

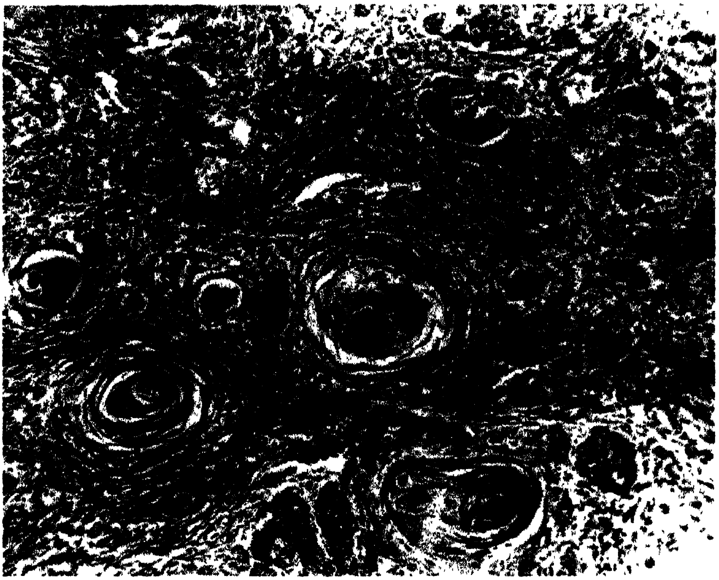


2

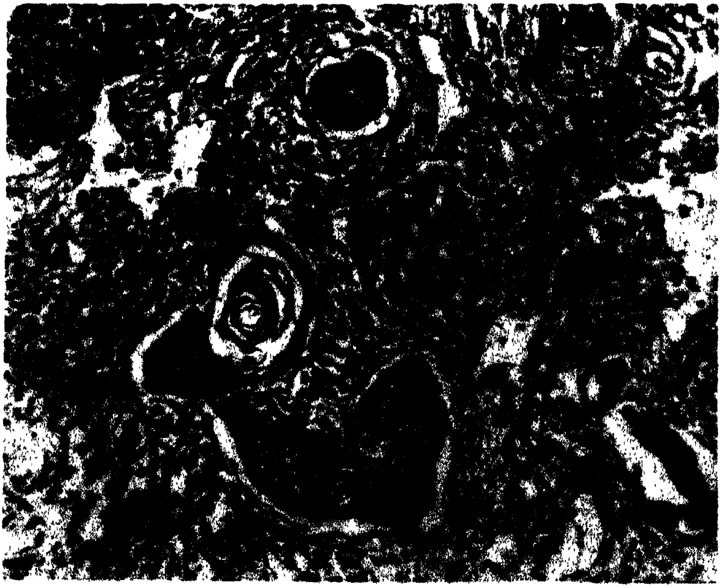


3

Carcinoma of Tonsil in a Common Wolf (*Canis lupus*).



4



5

Carcinoma of Tonsil in a Common Wolf (*Canis lupus*).

2. Carcinoma of the Tonsil in a Common Wolf (*Canis lupus*). By H. Harold Scott, M.D., F.R.C.P.London, F.R.S.E., F.Z.S., Milner Research Fellow in Comparative Pathology, London School of Hygiene and Tropical Medicine; Pathologist to the Zoological Society of London.

[Received November 14, 1927: Read February 21, 1928.]

(Plates I.-III.*)

No works on veterinary pathology which I have been able to consult make any mention of primary malignant disease of the tonsils as occurring among domesticated animals, nor can I find any reference to such as being found in captive wild animals. Cases are by no means frequently encountered even in Man—hence the following is deemed worthy of record.

A female Wolf, *Canis lupus*, which had been in the Gardens of the Society since July 14th, 1922, was removed to the Sanatorium towards the end of April 1927, on account of a large discharging wound in connection with a swelling in the right side of the neck and throat. The animal appeared to be in considerable distress and, perhaps pain, and would allow no one to approach it; it was, therefore, killed on April 30th and an autopsy was performed immediately afterwards.

The glands on the right side of the neck were swollen and hard, although they contained breaking down necrotic foci, and the surrounding muscles and tissues were hard and infiltrated. There was an ulcer with irregular ragged margin, the external opening of which measured 8 cm. in length by 3 cm. in its greatest width, and discharged foul blood-tinged pus. These enlarged and breaking down glands were secondary to a growth of the right tonsil. The tonsil itself had practically disappeared (Pl I. fig. 1), and its place was occupied by a depressed ulcer with an uneven base and a hard, in parts fungating, growth with eroded and everted border. From this a sinus extended to the enlarged and necrotizing glands. The tonsillar erosion was about the size of half-a-crown. The faucial pillars were practically uninvolved; the base of the tongue was free from growth, and the left tonsil was quite normal.

The condition, pathologically, was a malignant neoplasm of the right tonsil, with secondary invasion of the cervical glands, infiltration into the surrounding structures, adhesion to the overlying cutaneous tissues and breaking down to open externally by a ragged ulcer.

---

* For explanation of the Plates, see p. 47.

Microscopically, the picture presented was most interesting. From the general characters and the widespread infiltration of the squamous epithelial cells growth must have originated, not in the parenchymatous tissue of the tonsil itself, but in its epithelial covering. We see groups and masses of epithelial cells, some in small aggregations, others in large strands, penetrating and insinuating themselves into the lymphoid tissue of the tonsil (Pl. II. fig. 2). Between the islets of the carcinomatous cells there is a fairly well-developed stroma and the cells in many places tend to assume an alveolar disposition, in others they appear as branching columns. Where the fibrous stroma is abundant the enclosed areas of true growth show necrosis in varying degree.

Parts of the growth demonstrate very well the polymorphic development of carcinomatous cells and the anaplastic changes which are a common feature of many malignant epithelial neoplasms. Thus, in places we can almost trace the stages of transition from the usual rounded type of squamous cell to the drawn-out spindle-cell (Pl. II. fig. 3 & Pl. III. fig. 4). Again, at the periphery of some of the ingrowths of the neoplasm the cells are seen to be separated, becoming more loosely disposed, perhaps frayed out, and a picture strongly suggestive of a sarcomatous change of stroma is presented.

The lymphoid tonsillar remnants are, in most areas where they are present, easily distinguishable from this loosening of carcinomatous cells and polymorphism by the closeness with which the glandular lymphoid cells are packed. In some situations the advancing clump of epithelial cells is almost abruptly surrounded by such masses of small round lymphoid cells, which I take to be the normal lymphoid tissue of the gland being invaded but not yet replaced by the growth.

Anaplasia is further evidenced by the defective keratinization in considerable areas of the growth, though in other parts this is fairly marked and cell-nest formation extensive (Pl. III. figs. 4 & 5).

Yet one other point of interest is presented--namely, the re-differentiation which exists, some of the squamous epitheliomatous foci becoming transformed into apparent adenocarcinomatous islets.

Where we know practically nothing of the history, as in this case, owing to the impossibility of examination during life, we can only infer that the rate of growth in the original site was probably not very rapid; in some parts the stroma is relatively abundant and not very vascular, but, on the other hand, only a few giant-cells are met with. There was very likely, as is not unusual, different rates of growth in different parts of the tumour, for, in contrast with what has just been mentioned, in other sites the stroma is much less and, moreover, is quite richly cellular.

Opinions are at variance regarding the frequency of neoplasms of the tonsils in Man, but, generally speaking, it would appear that tumours of these glands are uncommon. Of the benign forms papillomata and fibrous polyps occur, while both carcinomatous and sarcomatous forms of malignant growth are met with. According to Kettle, the tonsil is liable to two forms of sarcoma—namely, the round-celled and the lymphosarcoma,—while Beattie and Dickson speak of a lymphosarcoma and a mixed-celled sarcoma. The dubious group, endothelioma, has also been described as occurring in the tonsil.

With regard to carcinoma, arising, of course. in the epithelial covering of the gland, the tumour is generally a squamous epithelioma developing either from the cells of the surface or in a tonsillar crypt. Bland-Sutton states that squamous-celled cancer arising in the faucial pillars or in the tonsil is not uncommon, but Beattie and Dickson maintain that, though the condition does occur, it is nearly always a secondary involvement in the tonsil. In such. the primary site is usually the base of the tongue or the pillars of the fauces.

Authorities are, however, practically unanimous in noting the rapidity of growth, the early extension to adjacent structures, and involvement of the regional lymphatic glands. In human cases destruction is great and the pillars of the fauces and the palate are often implicated and there is a tendency to invasion of the tongue. As regards the exact site or source of origin, this is often undetermined; the epithelioma may arise in the posterior part of the tongue, in the pharyngeal epithelium, or in that of the tonsil. In fact, it may grow in any part of the mouth and when in the posterior regions nearly always invades the fauces and the tonsils. In Man the course is rapid, death occurs within the year, often in six to eight months, the immediate cause being a septic pneumonia, a profuse hæmorrhage from erosion of a large vessel, or œdema of the glottis. The rate of growth, however, is very variable; it has been shown to be rapid in a well-developed man of middle age, and glands are involved early, whereas in those of advanced years it may be remarkably slow. Thus, a case is on record of a man of 70 in whom the disease had been present for three years; nevertheless, destruction was not great and the glandular involvement was slight.

In the vast majority of animals—I speak particularly of wild animals,—the age is a matter of conjecture, unless birth has taken place during the mother's captivity. Yet, again, we are still quite in the dark as to the correspondence, if any exists, between the age of an animal and that of man. Even in human cases the age at which the condition has been met with varies within very wide limits. L. H. Smith states that among his forty cases there were twenty-four between 50 and 60 years of age, the limits being 28 and 82, and the average 55 years. The youngest patient he could trace was only 18 years old.

In wild animals the rapidity of growth of a neoplasm can only be seen in its terminal stages. A thyroid tumour may, after it appears as a definite swelling, rapidly progress in a wild animal to a fatal issue, but we do not know how long it had been in existence before it attained a size sufficiently great to attract the attention of those in charge, for it is only objective signs of which we can take cognizance. So with the present case. After a residence in the Gardens of nearly five years, a discharging wound was noticed in the neck which was the result of a secondarily involved broken-down gland opening on the surface. How long the growth had been in existence prior to this it is impossible to state. The attention of the keeper had not been drawn to it from any difficulty in the taking of food and there was no noticeable emaciation. We can only infer, therefore, that the growth had been of rapid evolution. Those observers who have met with a large number of cases in Man have noted the much greater preponderance among males. Thus L. H. Smith found that of forty cases thirty-six were males, and Wurtz puts the proportion of males to females as high as 24 to 1. It is, perhaps, strange that the wolf, the subject of this paper, was a female.

Perusal of the records of human cases supplies a potent warning against applying too strictly to animal disease the factors which have been deemed causally active in Man. Thus Wurtz holds that there is a very definite relation between syphilis and carcinoma of the tonsil, and Stuart Low is quoted as having noted fifteen cases, all of which were syphilitic. L. H. Smith states that in 75 per cent. of cases there is a history of excessive use of tobacco, a fact remarked also by Wurtz. Carious teeth are recorded as being found in 50 per cent., as if this were also a factor, together with pyorrhœa. Such conditions cannot, however, be regarded as an unusual concomitant of any disease which occurs in persons averaging 55 years. The teeth of the wolf in question were remarkably sound. Other factors ætiologically implicated are the frequent taking of hot food and the habit of eating salt to excess at meal-times. The only evidence adduced for the former is that carcinoma of the tonsils is common amongst the Chinese, where the men partake of their food before the women. It may be confidently stated that none of these factors played any part in producing the carcinoma of the tonsil in this wolf.

REFERENCES.

ASCHOFF, L. Pathologische Anatomie. 4th Ed. 1919, vol. ii. p. 786

BARR, R. E. Carcinoma of the Tonsil. Med. Rec. & Ann. 1925, vol. xix. p. 486.

BEATTIE, J. M.; and DICKSON, W. E. C. Text-book of Pathology. 3rd Ed. 1925, p. 743.

BLAND-SUTTON, Sir J. Tumours Innocent and Malignant. 7th Ed. 1922, p. 336.

BOWLBY, Sir A. A., and ANDREWES, Sir F. W. Surgical Pathology and Pathological Anatomy. 7th Ed. 1920, p. 510.

Ewing, J. Neoplastic Diseases, 1919, p. 824.

Jacques, P. Cancer of Tonsil and Tongue. Presse med. 1925, vol. xxxiii. pp. 1617–18.

Kettle, E. H. The Pathology of Tumours. 2nd Ed. 1925, pp. 117, 223.

MacCallum, W. G. Text-book of Pathology. 2nd Ed. 1922, p. 1025.

Quirin, A. Epithelio-myosarcome de la Région amygdalienne. Bull. de l'Assoc. franç. pour l'étude du Cancer, 1925, vol. xiv. pp. 471–480.

Ross, M. Squamous-cell Carcinoma of Tonsil. Laryngoscope, 1925, vol. xxxv. pp. 15–20.

Schmaus, H. Grundriss der pathologischen Anatomie. 7th Ed. 1904, p. 391.

Wurtz, W. J. M. Malignant Disease of the Nose and Throat, with Special Reference to Cancer of Nasal Fossæ, Nasopharynx, and Tonsil. New York Med. Journal, 1921, vol. cxiii. p. 434.

Smith, L. H. Epithelioma of the Tonsil. New York State Journal Med. vol. xxiv. No. 7, pp. 289–292.

EXPLANATION OF THE PLATES.

Plate I.

Fig. 1. Photograph showing the normal tonsil on the left side, and on the right a ragged epithelioma replacing the tonsil and invading the surrounding tissues.

Plate II.

Fig. 2. Microphotograph of section of growth in tonsil showing infiltrating groups of squamous epitheliomatous cells. To the left and below are remains of tonsillar lymphoid tissue. (× 120.)

Fig. 3. Portion of the same under higher magnification (× 160). Epitheliomatous cells disposed in strands and some alveolarly; surrounding parts compressed and revealing here and there a tendency to spindle cell formation, partly, perhaps, the connective tissue of the tonsil, partly transformed carcinomatous elements.

Plate III.

Fig. 4. Section of cervical gland, secondarily invaded (× 120). Scattered masses of epitheliomatous cells with interspersed spindle-celled sarcoma-like transformation. Remnants of lymphoid glandular tissue present here and there. Foci of keratinization and cell-nest formation seen.

Fig. 5. Portion of the same under higher magnification (×160) showing the features described above.

Fig. 1 was taken from the specimen by Mr. F. Pittock in the laboratory at University College, by kind permission of Professor J. P. Hill, F R.S., the microphotographs (figs. 2–5) by Mr. F. Martin-Duncan, F.R.M.S., F.Z.S. I wish here to express my indebtedness to them for their kindness.—H. H. S.

3. On some Points in the Structure of Palæoniscid and allied Fish. By D. M. S. Watson, F.R.S., F.Z.S.

[Received November 11, 1927; Read February 21, 1928.]

(Text-figures 1–15.)

In a paper published in 1925 I was able to add certain facts to the knowledge of the structure of those early Actinopterygians which are included in the Palæoniscidæ which we owe to Traquair, Smith Woodward, Goodrich, Moodie, and Stensio. Since then further materials have come into my possession which enable me to clear up certain points which remained obscure in our knowledge of the neural cranium and lower jaw, and to add some sporadic observations, which indicate how large are the structural variations which may occur within the group.

Part 1.

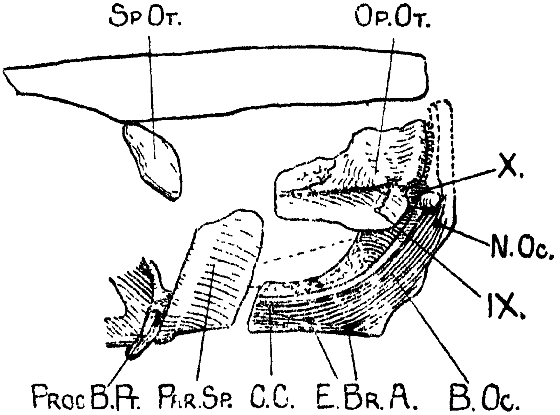
The neural cranium of a Palæoniscid was first described by Stensio in the Triassic *Birgeria*; subsequently I was able to give a more complete account in two Coal-Measure forms, neither capable of generic identification. In these two animals ossification was so complete that it was impossible to determine the individual elements which composed them, and a less completely ossified specimen of *Elonichthys aitkeni* was unsatisfactorily preserved.

A specimen of *Cosmoptychius striatus* preserved in an ironstone nodule from the Lower Carboniferous of Wardie beach shows the structure well preserved, and as it is of small size is incompletely ossified and allows the individual bones to be described.

The parietals, frontals, supra- and inter-temporals are present, naturally articulated but somewhat flattened. The endochondral elements of the skull lie nearly in their natural position, but have sunk down so that the actual depth of the whole is considerably reduced—in text-figures 1–3 they are placed in what appears to be their original relationship.

The occipital bones are already indistinguishably fused, and much of the upper part of the occiput above the foramen magnum is lost. The general structure is exactly as in the form I have already described. The foramen magnum is large and circular, the floor of the brain-case being ossified only for a very short distance in front of it. The occipital plate is wide, narrowing very suddenly at the level of the base of the brain. There is a pair of small foramina for occipital nerves (z) passing outward and downward to open on the outer surface on that part of the exoccipital which projects behind the general level of the occiput.

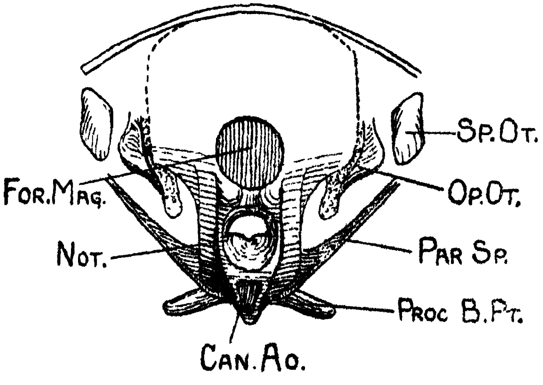
Text-figure 1.



Cosmoptychius striatus. Lower Carboniferous, Wardie Beach. Lateral surface of the neural cranium. × 4. The bones have been replaced in their original position.

B.Oc.=Basioccipital. C.C.=Carotid foramen. E.Br.A.=Foramen for epibranchial arteries. N.Oc.=Foramen for the occipital nerve z. Op.Ot.=Opisthotic. Par.Sp.=Parasphenoid. Proc.B.Pt.=Processus basipterygoideus. Sp.Ot.=Sphenotic. IX.=Foramen for the glossopharyngeus. X.=Foramen for the vagus.

Text-figure 2.



Cosmoptychius striatus. Occipital aspect of the neural cranium. × 4.

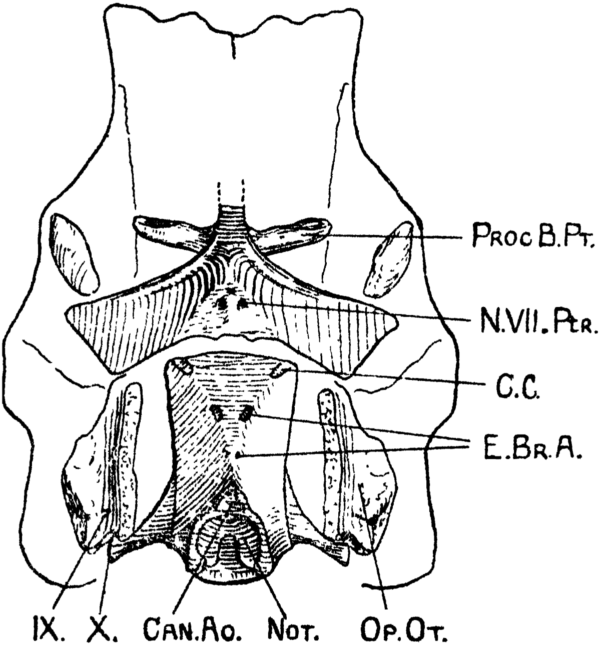
Can.Ao.=Aortic canal. For.Mag.=Foramen magnum. Not.=Pit and groove for the notochord. Op.Ot.=Opisthotic. Par.Sp.=Parasphenoid, ascending ramus. Proc.B.Pt.=Processus basipterygoideus. Sp.Ot.=Sphenotic.

The anterior face of the occipital plate is completely ossified; it presents a concavity directed outward and forward which faces the otic capsule.

The pit for the notochord extends forward to the extreme anterior end of the basioccipital, but in front it is represented merely by a groove, the upper part of the basioccipital being still cartilaginous.

There is an aortic canal which tunnels the basioccipital below the notochord, and splits anteriorly to open by a pair of widely-separated common carotid foramina. A small posterior and larger anterior pair of foramina for the entrance of epibranchial arteries enter the aortic canal.

Text-figure 3.



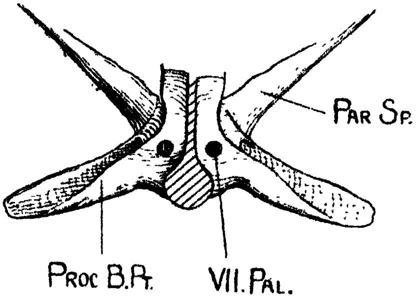
Cosmoptychius striatus. Neural cranium, ventral view. × 4.

C.C.=Foramen for the common carotid. CAN.AO.=Aortic canal. E.BR.A.=Foramina for epibranchial arteries. N.VII.PTR.=Foramen for the pretrematic branch of the facialis. NOT.=Notochord. OP.OT.=Opisthotic. PROC.B.PT.=Processus basipterygoideus. IX.=Glossopharyngeal foramen. X.=Vagal foramen.

The basisphenoid is incompletely ossified; it consists of a small mass of bone lying tightly attached to the upper surface of the parasphenoid. Anteriorly it forms part of the incomplete interorbital septum, whose hinder border is continuous with a transverse plate of bone which turns forward as it rises in the skull. Ventrally the outer margins of this bony plate are produced into long basipterygoid processes, which bear a depressed area for articulation with the palato-quadrate on the upper and anterior faces. The root of each basipterygoid process is perforated by a foramen which leads into a canal, running backward, upward, and outward in the basisphenoid until it leads into a groove on the upper surface of the processus ascendens of the parasphenoid.

From this canal a branch passes downward and inward to perforate the parasphenoid and open on the ventral surface of the skull. The main canal must have transmitted the palatine branch of the Facial nerve, the branch being for a ramus pretrematicus, passing to the skin of the mouth, as Herrick has described it in *Menidia*.

Text-figure 4.



Cosmoptychius striatus. Parasphenoid and basisphenoid viewed from in front. × 7.

Par.Sp. = Parasphenoid, ascending ramus. Proc.B.Pt. = Processus basipterygoideus. VII.Pal. = Foramen for the palatine branch of the VII. nerve.

The dorsal surface of the basisphenoid behind the basipterygoid possesses a very deep narrow pit, which nearly but not quite meets a similar pit in the parasphenoid. These clearly represent a canal for a hypophysial duct, which had become cut across shortly before the death of the animal.

Still further back the dorsal surface bears a pair of irregular shallow depressions, which may indicate the attachment of the external recti. Finally, the bone ends in a nearly vertical surface, which in life was separated from the similar anterior end of the basioccipital by about 1 millimetre of cartilage. This posterior surface has a median notch for the reception of the notochord.

Fragmentary as it is, there can be no doubt that this basisphenoid is identical in important morphological characters with those of the two Palæoniscids I have already described. It is clear that a functional myodome was present and that this must have been roofed by a cartilaginous bridge, which may have been ossified either from the basisphenoid or the prootic.

The only bones in the ear-capsule which are well enough preserved for description are the opisthotics, the bones called "prootico opisthotic" by Stensio.

Each of these bones has a completely ossified external surface and posterior end, but on all other faces it passes irregularly into cartilage. Posteriorly the opisthotic has a segmental border which faced at a very small distance the front of the occipital region. The border bears a distinct notch for the vagus. The evidence of the neural crania which I have previously described shows that the vagal foramen lies just above the sudden expansion of the occipital plate, so that the position of the opisthotic with respect to the occiput is fixed.

Below the level of the vagal foramen the bone is represented by a thin flange lying on the outer surface of the saccular portion of the inner ear. This flange has a thin and clearly incompletely ossified lower border, which forms the upper limit of the very large vestibular fontanelle. Towards its hinder end the flange is perforated by a small glossopharyngeal foramen from which a small groove, presumably for the lateralis component of that nerve, passes dorsally.

The dorsal part of the opisthotic is much more massively ossified. Its outer surface turns outwards so as to overhang the lower part of the bone and form a groove in which the vena capitis lateralis lay. The surface then becomes vertical, forming the great longitudinal ridge which extends from the postorbital process to the hinder end of the otic region. Posteriorly this ridge is truncated by a depressed area on the lateral surface of the bone, into which the groove from the glossopharyngeal foramen leads. On the inner surface the cast of the lower half of the posterior vertical semicircular canal is shown, making it certain that this part of the labyrinth was completely surrounded by bone. No definite trace of the horizontal canal is visible.

Comparison with other Palæoniscid brain-cases makes it clear that ossification had not extended into the region of the anterior semicircular canal at any point.

A small bony process extends inward toward the middle line from the upper part of the hinder half of the opisthotic—this apparently passes through the loop formed by the posterior canal.

There is no trace of any other ossification in the otic region.

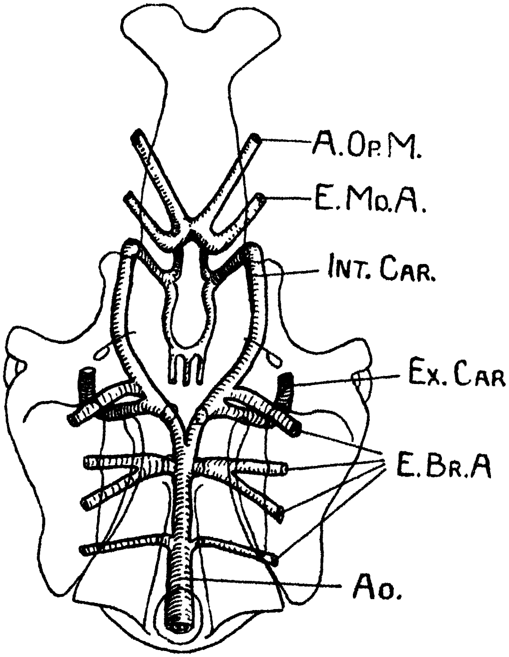
Far anteriorly in front of the upper end of the ascending process of the parasphenoid lies a relatively large and massive bone, whose margin forms a postorbital process. This is the anto-sphenotic.

It is obvious that the incompletely ossified brain-case which I have just described is identical in its general morphology with those of other Palæoniscids.

It differs from Palæoniscid A of my former paper in the perforation of the basiphenoid by the palatine branch of the VII. nerve, whilst Palæoniscid B differs from it by the posterior position of this foramen, which in it not only perforates the basisphenoid, but issues on the lower surface behind the parasphenoid.

The most important fact which arises from the specimen is,

Text-figure 5.



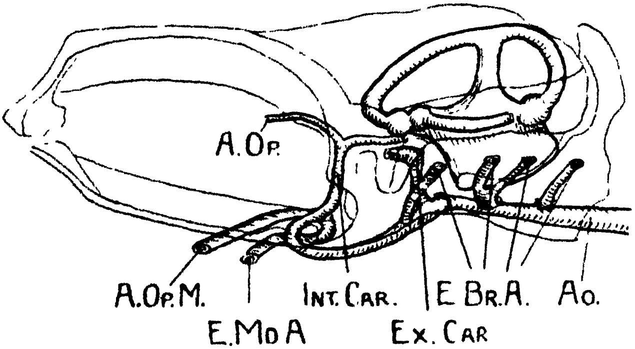
Palæoniscid A. Outline of the neural cranium with the arterial system as far as it can be determined from foramina and grooves. Viewed from below. × $\frac{10}{3}$.

A.Op.M. = Arteria ophthalmica magna. Ao. = Aorta. E.Br.A. = Efferent branchial arteries. E.Md.A. = Efferent mandibular artery. Ex.Car. = External carotid. Int.Car. = Internal carotid.

however, that the chief ossification in the otic capsule is the opisthotic, the prootic region being still entirely unossified. The only parallel to this arrangement which is known is in *Polypterus*.

The interpretation of the imperfectly ossified and somewhat displaced elements in this skull of *Cosmoptychius striatus* was only rendered possible by knowledge of the similar skulls I have described previously; and an understanding of the nature of the foramen for the VII. nerve can only be reached on comparison with the vascular arrangements which are displayed in those specimens. I therefore give in text-figs. 5 and 6 outline drawings of the neural cranium of Palæoniscid A with the arterial system represented in relation to it so far as its distribution can be deduced from the foramina and other indications on the bony

Text-figure 6



Palæoniscid A. Neural cranium from the side with the cavity for the internal ear, represented as a cast, and the arterial system. Viewed from the left side. $\times \frac{10}{3}$.

A.Op. = Arteria optica. A.Op.M. = Arteria ophthalmica magna. Ao. = Aorta. E.Br.A. = Efferent branchial arteries. E.Md.A. = Efferent mandibular artery. Ex.Car. = External carotid. Int.Car. = Internal carotid.

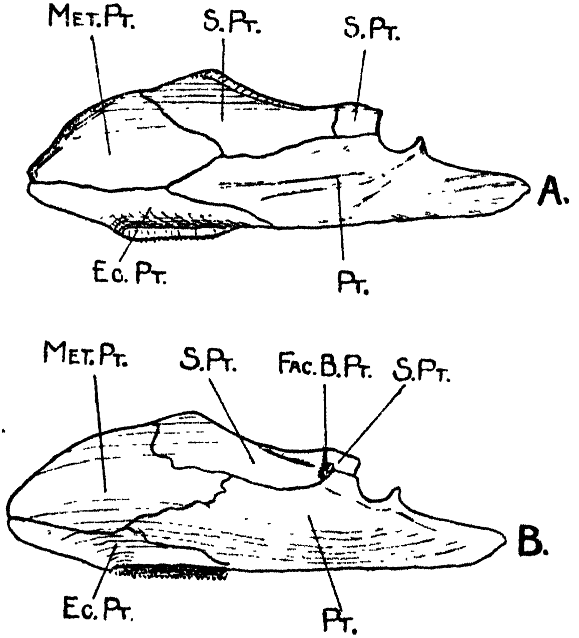
skulls. In text-fig. 6 I have introduced also an outline of the spaces which housed the internal ear in order to make clear the spatial relations of that organ.

It will be clear that in general the arteries of the head conform extraordinarily closely to those found in the modern Ganoids and Teleosts.

Part 2.

In my previous paper I gave an account of the structure of the palate of *Nematoptychius*, to which I can now make additions. It is clear that there are small differences in structure between the different individuals, which are ignored in the following account. The pterygoid has the structure already described, but has not in any of the new specimens shown the anterior ridge and notch which I interpreted as evidence of an internal nostril. The metapterygoid is shown to include the element which in my former specimen I interpreted as a second suprapterygoid. The "first" suprapterygoid has a curiously thickened and obliquely facetted dorsal border, and ends anteriorly by a vertical suture with a small anterior suprapterygoid, whose anterior border forms the posterior margin of a deep notch or notches for the passage of the fifth nerve. On its inner surface this suprapterygoid bears a facet raised a little above its surface for articulation with the basipterygoid process. The occurrence of this articulation behind the V. nerve in *Nematoptychius*, whilst in all other Palæoniscids known to me it lies in front of that nerve, is of importance, in that it serves to establish the homologous nature of the basipterygoid process in Palæoniscids and Osteolepids.

Text-figure 7.



Nematoptychius greenocki.

A. Palato-quadrate apparatus of the right side. Lateral view. × 1.
B. Palato-quadrate apparatus of the left side. Mesial aspect. × 1.
EC.PT.=Ectopterygoid. FAC.B.PT.=Facet for articulation with the basipterygoid process. MET.PT.=metapterygoid. PT.=Pterygoid. S.PT.=Suprapterygoid.

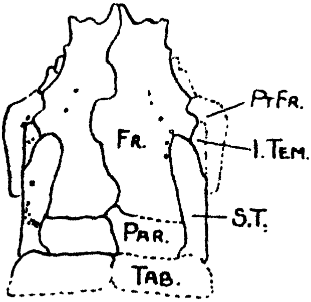
Part 3.

The structure of the external surface of the skull has been fully described in only few Palæoniscids, and as a comparison between this structure and that of corresponding regions of Holostei is difficult to establish, it seems to me important to describe certain other rather unusual Palæoniscids.

Elonichthys caudalis.

The specimen of which I have described the palate shows the structure of the dermal roof and side of the head with great clearness, although the individual bones are usually somewhat separated. This fish is remarkable for the thickness of its bones, which overlap deeply and accurately, so that there is no difficulty in restoring them to their proper places. The dorsal surface is flat, the frontals being very large bones, articulating by a most irregular suture. The parietals are very small, rectangular in shape, and shorter than they are wide. The supratemporal is a

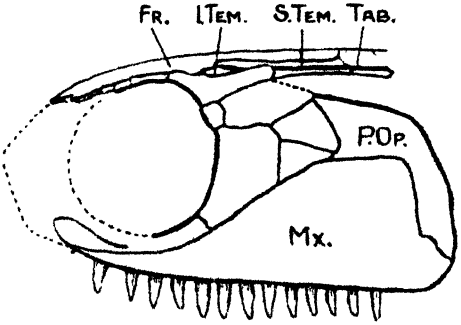
Text-figure 8.



Elonichthys caudalis. From the Rag Mine Ironstone, Fenton, Staffs. In the Museum of Practical Geology. Reconstruction of the roof of the skull, viewed from above. × ⅔.

Fr. = Frontal. I.Tem. = Intertemporal. Par. = Parietal. Pt Fr. = Post-frontal. S.T. = Supratemporal. Tab. = Tabular.

Text-figure 9.



Elonichthys caudalis. Reconstruction of the left side of the skull. × ⅔.

Fr. = Frontal. I.Tem. = Intertemporal. Mx. = Maxilla. P.Op. = Pre-opercular. S.Tem. = Supratemporal. Tab. = Tabular.

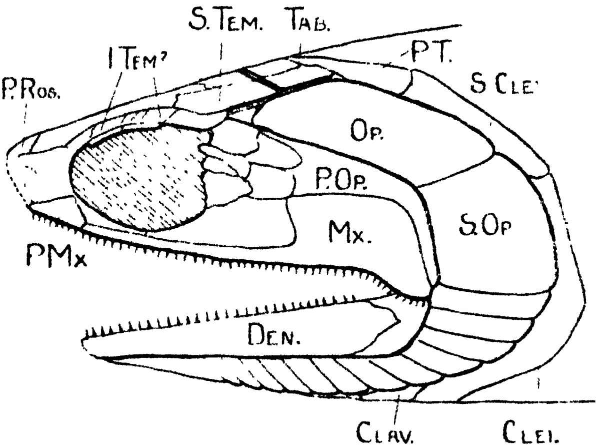
large bone articulated with the whole of the lateral border of the parietal and a large part of that of the frontal. The intertemporal is an extremely small bone wedged in between the supratemporal, frontal, and postfrontal. Its identification is certain, because the main lateral-line canal ends in it, and in its relations to surrounding elements and exclusion from the orbit it agrees well with the corresponding bone in *Cheirolepis*. It presents a great contrast to the large bone in *Coccocephalus*. The orbit is surrounded by a ring of bones uncertain in number, but clearly incapable of being identified individually with the circlet of five which surrounds the eye in the more primitive Osteolepids, Tetrapoda, and in *Coccocephalus* and *Cheirolepis*. Between the posterior elements of the circumorbital ring and the anterior border of the preopercular lies a series of three bones, which are unrepresented in *Cheirolepis*, present in the form of a single element in *Coccocephalus*, and are shown as postorbitals in Traquair's figure of *Palæoniscus* and in White's figure of *Ætheretmon* and in some other forms. These bones may perhaps be homologous with some of the cheek-plates in such Osteolepids as *Holoptychius*, but are clearly far too variable in character to receive individual names. They are, however, of importance, because they provide the source from which the nearly universal two postorbitals of the Holostei have been derived.

Oxygnathus ornatus.

The external structure of the head of *Oxygnathus ornatus* can be made out completely from comparison of the numerous specimens from the Lower Lias of Lyme Regis, in the British and Jermyn Street Museums. The specimens in the latter Museum are the more important. I have already described the structure of the dorsal surface of the skull, which is remarkable for its great width and for the apparent absence of an intertemporal. It is possible that my original interpretation of a series of small bones lying above the orbit as separated fragments of an intertemporal is correct. But it is perhaps more probable that this element has entirely vanished in the way suggested by its great reduction in *Elonichthys caudalis*. The circumorbital series of bones is composed of numerous elements. Two of these, which lie in contact with the dorsal margin of the very slender anterior end of the maxilla, are constant. Those which close the orbit behind vary in number and in shape, but are always separated from the anterior end of the preoperculum by other bones. The lachrimal is a very large delicate bone whose relations to the rostral and nasal cannot be determined, although its suture with the premaxilla is clear.

I have already shown that *Oxygnathus* is peculiar amongst Palæoniscids, in that the main lateral-line canal is continuous with the hinder end of the supra-orbitral canal. *Elonichthys* *caudalis* may show an intermediate stage. In it the supraorbital canal ends in the frontal immediately mesial of the supratemporal, instead of passing on, as usually, well clear of that bone into the parietal.

Text-figure 10.



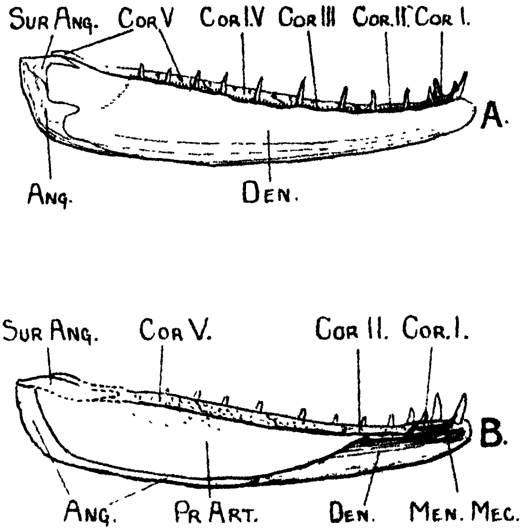
Oxygnathus ornatus. Lower Lias, Lyme Regis. Left side of the head. Reconstructed from specimens in the Jermyn Street Museum and in my own collection. × 1.

Clav.=Clavicle. Clei.=Cleithrum. Den.=Dentary. I.Tem.?=Intertemporal? Mx.=Maxilla. Op.=Operculum. P.Mx.=Premaxilla. P.Op.=Preoperculum. P.Ros.=Postrostral. P.T.=Post-temporal. S.Clei.=Supracleithrum. S.Op.=Suboperculum. S.Tem.=Supratemporal. Tab.=Tabular.

Part 4.

The lower jaw of Palæoniscids is still badly understood, but from materials of *Nematoptychius* in my own possession, most of which have been prepared by removing the bone so as to leave impressions in the Ironstone, it is possible to make out the whole structure, except for the articular bone. The surangular has a small exposure on the outer surface, but actually extends forward for a very considerable distance. Throughout its lower edge it is overlapped by the upper border of the angular, and its outer surface is very largely concealed by the attached dentary. The upper border is surmounted by the hinder end of the fifth coronoid, nearly to the region of the articular. The angular reaches upwards behind the surangular nearly to the articulation, and extends forward about halfway to the anterior end of the jaw. Its lower border is free, not turned up at all on to the inner surface of the jaw, but is visible on that aspect owing to the shallowness of the pre-articular. The dentary is an immense bone of very familiar character—anteriorly it has a somewhat indefinite synthesis with its fellow and then passes backward deepening as it goes, forming a shell of thin bone on the outer surface, overlapping very extensively both the angular and surangular. The upper border supports a series of widely-spaced large teeth, labial to which lies a tight-set row of tiny denticles. The large teeth are set on a shelf passing inwards from the body of the bone. This shelf terminates in front at the synthesis and

Text-figure 11.



Nematoptychius greenocki. The lower jaw from a series of specimens from the Lower Carboniferous of Wardie Beach, Midlothian.
A. Outer surface. × 1. B. Inner surface. × 1.
Ang.=Angular. Cor.I.–V.=Coronoids. Den.=Dentary. Men.Mec.=Mentomeckelian. Pr.Art.=Prearticular. Sur.Ang.=Surangular.

overhangs a deep groove, within which lies Meckel's cartilage. The admesial border of this shelf is in contact throughout a good deal of its length with the upper border of the pre-articular, and the suture between the two elements is covered by the continuous chain of coronoids.

The anterior coronoid is a small rectangular bone lying close up to the synthesis, and supported in part by the shelf which projects inwards from the dentary. It carries a single large tooth, and apparently, though not certainly, a pit for a replacing tooth of Osteolepid pattern. The next three coronoids are similar in structure, together they form a strip of bone which projects dorsally as a wall lying parallel to and a little within the series of large teeth in the dentary. This wall extends to about half the height of the dentary teeth, and is only half as thick as it is high. The groove between these teeth and the coronoids receives a ridge on the ectopterygoid and palatines, when the mouth is closed. The labial surface of these coronoids is smooth, but there is a series of shallow depressions. The lingual surface is covered with a close-set shagreen of small rounded denticles. The anterior end of the fifth coronoid agrees exactly in its character with those which precede it, but posteriorly the bone splits so as to surround the supra-Meckelian fossa anteriorly, and then passes backwards above the surangular and pre-articular. The pre-articular is a large bone extending forward from its attachment to the articular for three-quarters of the length of the jaw. Its upper border is in contact with the coronoids and dentary for the greater part of its length, whilst nearly the whole of its lower margin is free, although posteriorly it seems to join the angular.

The structure of the articular cannot be ascertained, but it is clear that the posterior half of Meckel's cartilage is completely though very lightly ossified. This bone is of unexpected depth, very nearly filling the cavity of the jaw. Anteriorly just behind the synthesis is a small independent Mento-meckelian bone.

This jaw agrees in all important structures with that of *Elonichthys caudalis*, but differs from it in the curious wall formed by the coronoids, in exactly the same way that the palatines of the two fishes differ.

The lower jaw of *Nematoptychius* shows a special recessed area on the outer surface of the dentary surangular and angular which is free from ornament and receives the hinder end of the lower margin of the maxilla. This feature is found in the majority of Palæoniscid and Platysomid lower jaws.

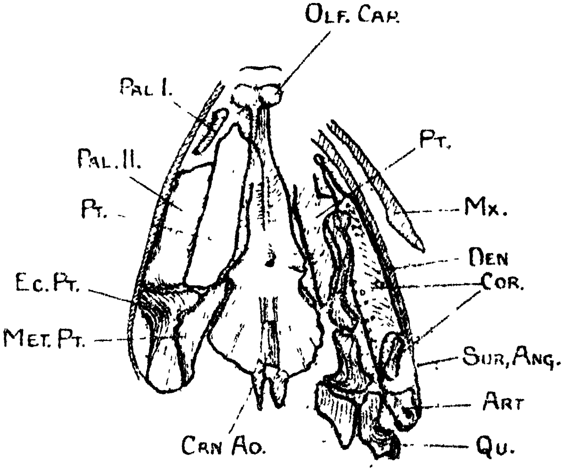
Part 5.

Eurynotus crenatus.

A specimen of *Eurynotus* from the Lower Carboniferous of Wardie Beach in my own collection is of importance, because it shows the structure of the greater part of the palate. Previously this region has been known only from an unintelligible specimen figured by Traquair (1880), and is otherwise only known amongt the Platysomids in *Cheirodus*.

The parasphenoid conforms in the main to the ordinary Palæoniscid pattern; it is widely extended into a pair of transverse rami which underlie the basicranial region. It appears probable, however, that, as in *Birgeria*, *Saurichthys*, and the Sturgeons, it extends a good deal further back than in most Palæoniscids, so that it underlies the basi-occipital. As preserved, the hinder part of the parasphenoid forms a flat sheet from which a deep and narrow ridge descends vertically in the middle line. This ridge is tunnelled by the aortic canal, which for a considerable part of its course seems to lie entirely within the parasphenoid. In the region of the myodome, which cannot be shown to have existed, the parasphenoid possesses a pit which may actually be a foramen, and is in any case to be associated with a hypophysial duct. It is impossible to be certain whether a basipterygoid process was present or not. Certain indications on both sides of the specimen suggest that the process formed a slight outstanding projection of the normal Palæoniscid type. In the front of this region the parasphenoid is wide, but it

Text-figure 12.



Eurynotus crenatus. The palate and parasphenoid and lower jaw. Viewed from above. From a specimen from Wardie Beach. × $\frac{4}{5}$.

Art.=Articular. Can.Ao.=Aortic canal. Cor.=Coronoid. Den.=Dentary. Ec.Pt.=Ectopterygoid. Met.Pt.=Metapterygoid. Mx.=Maxilla. Olf. Cap.=Olfactory capsule. Pal. I. and II.=Palatines. Pt.=Pterygoid. Qu.=Quadrate. Sur.Ang.=Surangular.

rapidly narrows as it is traced forwards until in the ethmoidal region it forms little more than the lower edge of the internasal septum. The anterior part of the parasphenoid is continuous with an ossification in the interorbital septum, only the lower part of which is preserved. This septum appears to deepen as it is traced forward, and, finally, vanishes by passing into a mass of bone lying transversely in the skull, nearly in contact with the dermal roof. This mass consists essentially of two spherical structures which overhang the olfactory chambers, their lower surfaces being flattened and perhaps a little excavated for the reception of those sense-organs.

The quadrate, well shown on the right side of the specimen, is a small sheet of bone passing forward on the inner side of the fossa for the masticatory muscles and coming into contact with the ectopterygoid and the metapterygoid. The articular end of the quadrate is produced into a rounded condyle, which fits the articular surface in the articular. The metapterygoid is not completely preserved on either side of the specimen, but stood nearly vertically in the skull, articulating for the greater part of its length with the ectopterygoid in a completely Palæoniscid manner. As is customary in Palæoniscids, the ectopterygoid may be divided into two regions—that which extends backwards to the quadrate and is in contact with the metapterygoid, standing nearly vertically in the skull, and the palatal portion, which lies horizontally and is connected by suture with the palatine. In the present specimen it is clear that this ramus of the ectopterygoid has also an attachment to the pterygoid.

The palatine series of bones appear to consist of two elements—the posterior is much the larger, being extremely thick, with the whole of its palatal surface covered with close-set small crushing-teeth. This bone is held rigidly in position, because a strip of the lateral part of its lower surface is supported by a flange passing inwards below it from the inner surface of the maxilla, exactly as in Palæoniscids. The anterior palatal element is misplaced and shown only in section. It also is massive and appears, so far as may be judged, to have repeated the structure of the posterior element on a smaller scale.

The pterygoid, also an unusually massive bone, extends forward from its suture with the ectopterygoid and the metapterygoid until it terminates anteriorly in a point lying a little behind the post-olfactory plate. The lower edge of the palatal surface of the pterygoid is tooth-bearing. I have seen no indication of pre-vomers, which must have existed, and am reasonably sure that no suprapterygoids were present.

The palate just described differs from that of such a Palæoniscid as *Elonichthys semi-striatus* only in the loss of the anterior suprapterygoid and the increased massiveness of all the bones, which results from the development of a crushing dentition. On the other hand, the palate of *Cheirodus* is clearly a further development of that of *Eurynotus*, Traquair's pterygoid being a palatine and his metapterygoid probably including two elements, a pterygoid and a metapterygoid proper—an interpretation supported by Traquair's fig. 3 on pl. v., where the bone Y may be one of the two elements.

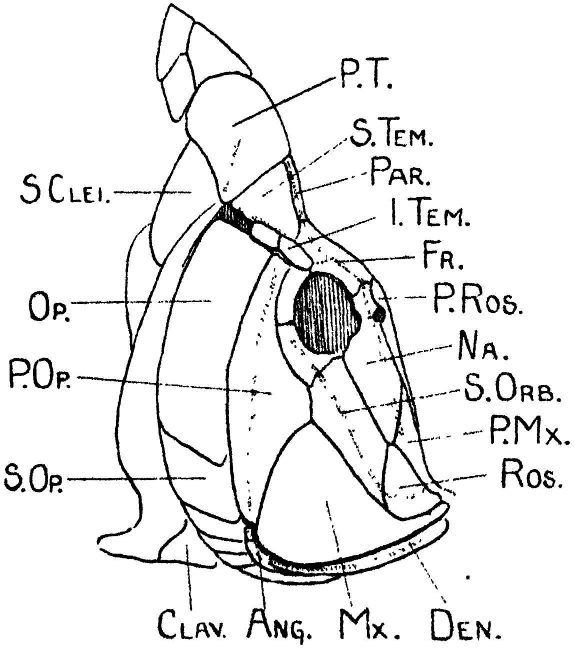
Lower Jaw.

The articular is shown as a massive bone bearing a sphæroidal pit for the quadrate on the upper surface at the hinder end. In front of this cavity the bone extends forwards for some considerable distance, and then terminates at a sharply-defined border behind the supra-Meckelian fossa. On the lingual surface it rises steeply and is overlapped by the hinder end either of the pre-articular or of the process of the posterior coronoid, which extends backwards in contact with the upper border of the pre-articular.

Platysomus.

The structure of the head in *Platysomus* was described by Traquair (1880) and represented in a restored figure. I am able to add to, and in some respects correct, this account on the evidence provided by two specimens of *Platysomus parvulus*, one of which is preserved almost uncrushed in an Ironstone nodule, the other flattened in shale. Both have been prepared by removing the bones with acid. The parietals and frontals have the form already described by Traquair, but the latter bone is

Text-figure 13.



Head of *Platysomus parvulus.* Restored from an uncrushed specimen in the Knowles Ironstone of Fenton, Staffs, with the aid of another specimen. × 2.

Ang. = Angular. Clav. = Clavicle. Den. = Dentary. Fr. = Frontal. I.Tem. = Intertemporal. Mx. = Maxilla. Na. = Nasal. Op. = Operculum. P.Mx. = Premaxilla. P.Op. = Preoperculum. P.Ros. = Postrostral. P.T. = Post-temporal. Par. = Parietal. Ros. = Rostral. S.Clei. = Supracleithrum. S.Op. = Suboperculum. S.Orb. = Suborbital. S.Tem. = Supratemporal.

very distinctly shown to form the upper border of the orbit, over which it is raised into a dome. The supratemporal is a strange triangular bone scarcely touching the frontal. The intertemporal attached to the lateral margins of the frontal and supratemporal differs a good deal in its shape from Traquair's figure. The postrostral and nasal are almost exactly as he described them, but the upper end of the facial process of the premaxilla, which is probably a rostral bone, separates the two for some considerable distance. The differences between my figure and Traquair's in this region depend on the fact that the bones overlap deeply, Traquair representing the inner surface and I the outer.

The orbit is bounded behind by two small bones, one of which articulates with the intertemporal, the other with the lachrimal. A displaced element shown in one of my specimens may have formed part of the orbital margin lying in a recess in the nasal bone—if so, this bone was a prefrontal. The lachrimal or suborbital forms a good deal of the face, it lies wedged in between the nasal and the maxilla, and its lower margin is in contact with a bone which may be variously interpreted either as a rostral or less probably as an anterior suborbital. The pre-operculum has the form already described by Traquair; the maxilla differs from his familiar drawing in the excessive slenderness of its anterior end, where it lies below the lateral rostral which rests in a rabbet on its upper edge. The large bone described by Traquair as a post-temporal articulates directly by an underlap with the parietal and supratemporal.

The opercular and subopercular are as Traquair has described them, but they differ a good deal in their relative heights in different individuals. The number of branchiostegals is uncertain, perhaps three in one specimen, and the anterior one is a large heavily ornamented plate. The clavicle and cleithrum are as Traquair has described them, but it is certain that the supracleithrum of his description is really two bones, one of which (rigidly articulated to the posterior surface of the upper end of the cleithrum) is an enlarged post-cleithral scale.

The lower jaw is a slender structure turned inwards towards its anterior end in such a way as to show that the premaxillæ lay nearly transversely in the head and that the snout was rounded and not pointed. Posteriorly the jaw is deep and raised into a low coronoid process; as in Palæoniscids the dentary extends very far back and forms the lower border of the jaw for a good deal of its length. The surangular and angular are not distinguishable, but a pre-articular is shown to form the inner surface of the jaw, posteriorly rising as it is traced fowards to articulate with the posterior coronoid, which passes backwards both labially and lingually to the supra-Meckelian vacuity. It is impossible from my material to discover whether other coronoids were present or not. The outer surface of the whole jaw shows a recess or unornamented region into which the posterior lower corner of the maxilla was received.

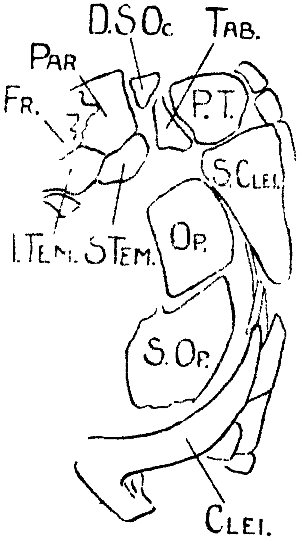
Lateral-line Apparatus.

The lateral-line canals are throughout extraordinarily fine, about a quarter of a millimetre in diameter. They communicate with the exterior by somewhat infrequent tubuli, whose openings can sometimes be seen. There is a canal in the post-temporal which runs directly upwards from the pointed lower extremity towards the middle line. This cannot, I think, be part of the main canal; it is more plausibly interpreted as the occipital cross-commissure, which would lead to the belief that the bone is really an enlarged tabular. In a specimen of *Wardichthys cyclosoma* (text-fig. 14), however, what is clearly the same element is separated from the parietals and supra-temporals by a row of four small bones, and is hence quite certainly the real post-temporal. I am thus inclined to believe that in *Platysomus*, with the disappearance of the tabular row, the post-temporal has extended forwards so as to enclose the occipital cross-commissure. The main canal passes forward through the lateral margin of the supratemporal and along the inner edge of the intertemporal to its suture with the frontal. The intertemporal is crossed by a deep groove, which appears to represent the upper end of the suborbital canal. This canal perforates the two postorbital bones, passes downwards almost vertically through the suborbital, and then turns forward horizontally through the rostral, apparently turning upwards at the anterior margin of that bone. The supraorbital canal begins, as Traquair has shown, at the hinder margin of the parietal; it continues forward through the frontal into the nasal, where it swings round laterally to the nostril, and then pursues a straight course down the nasal into that upper part of the premaxilla which is probably of rostral homologies. The anterior end of this canal is not shown. The hyomandibular canal extends from the upper to the lower corner of the pre-opercular, and is then continued in the mandible parallel to and immediately above its lower border. In one of my specimens a line of pores passes from the supraorbital canal across the frontal into the intertemporal, there joining the suborbital canal.

This more complete account shows that certain bones, the rostrals, which are not frequent in Palæoniscids, do occur in *Platysomus*; this occurence suggests that, like the Catopterids, these forms must have arisen from a primitive member of the Palæoniscidæ. The distribution of the lateral-line apparatus is essentially the same in the two families, but the connection between the supraorbital and suborbital canals is only known in *Oxygnathus* amongst the Palæoniscidæ.

The specimen of *Wardichthys* represented in text-fig. 14 shows that the operculum is considerably narrower than the suboperculum, and that the latter bone shows a distinct notch in its upper border, which must have received the lower end of the separate element lying between the anterior border of the opercular and the pre-opercular, identical with that which exists in many Palæoniscids—for example, in *Cheirolepis*, where it is usually called X. This is the first recorded occurrence of the

Text-figure 14.



Wardichthys cyclosoma Lower Carboniferous of Gullane. Posterior part of the left side of the head and shoulder-girdle. × 2.

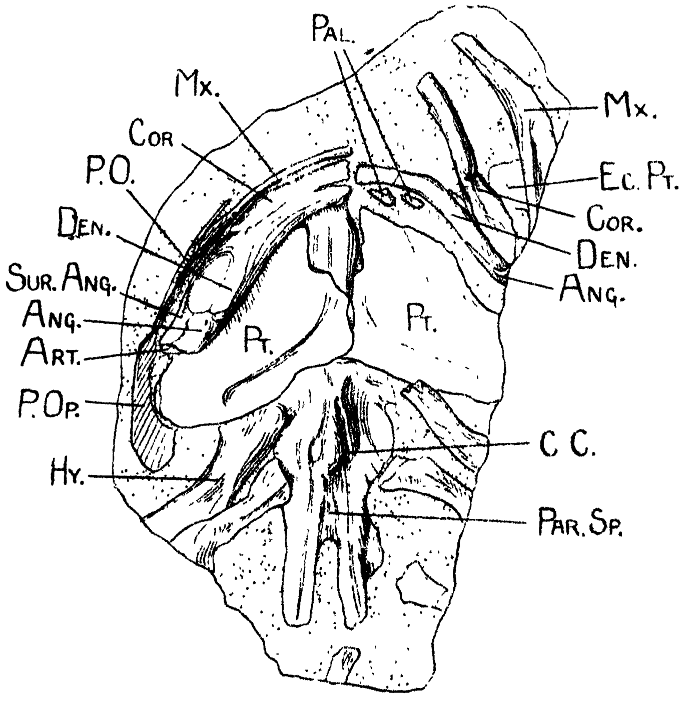
Clei.=Cleithrum. D.S.Oc.=Dermo-supraoccipital. Fr.=Frontal. I.Tem.= Intertemporal. Op.=Operculum. P.T.=Post-temporal. Par.=Parietal. S.Clei.=Supracleithrum. S.Op.=Suboperculum. S.Tem.=Supratemporal. Tab.=Tabular.

bone in Platysomids. It seems not impossible that *Wardichthys* may be somewhat more nearly related to *Benedenius* than to any other form.

Part 6.

The structure of the lower jaw of *Nematoptychius* may perhaps provide the explanation of a curious feature of the lower jaw of *Chondrosteus*, which has not previously been recognised. In *C. acipenseroides* there is a small lightly-ossified articular, to whose outer surface the short surangular is attached. The lower border of the jaw for about a third of its length is formed by the angular. The rest of the outer surface of the jaw has always been supposed to consist of a single large dentary, but actually is made up of two somewhat featureless bones lying above one another. That these bones are, indeed, separate is shown quite conclusively by one of my specimens, where they have separated and now lie at an angle with one another, and it is shown also by the fact that in several specimens of *C. acipenseroides*, and in both the Stuttgart and Tübingen examples of *C. hindenburgi*, their anterior ends have parted from one another so as to leave a narrow but perfectly distinct notch. In *Acipenser*, both in the adult and in larvæ of all stages, only a single bone is present in the corresponding position. It is clear that one of these two bones must be the dentary, and it is natural to suppose that this is the upper. The lower bone would therefore have to be a splenial, which does not occur in any known Actinopterygian, though it may perhaps have been present in *Cheirolepis*. The relations of this bone to the angular, which it overlies, are, however, never found existing between a splenial and the angular, and it is preferable to regard the lower bone as the dentary. The upper bone which

Text-figure 15.



Chondrosteus acipenseroides. Lower Lias, Lyme Regis. Ventral surface of the head. × ⅔ approx.

Ang. = Angular. Art. = Articular. C.C. = Foramen for the common carotid. Cor. = Coronoid. Den. = Dentary. Ec.Pt. = Ectopterygoid. Hy. = hyomandibular. Mx. = Maxilla. P.O. = Postorbital. P.Op. = Preoperculum. Pal. = Palatine. Par.Sp. = Parasphenoid. Pt. = Pterygoid. Sur.Ang. = Surangular.

articulates posteriorly with the surangular can only be a coronoid, and the conditions in *Nematoptychius* suggest that it gained this unusual position quite directly with the disappearance of the teeth on the dentary margin. Which bone persists in *Acipenser* it is impossible to say.

Text-fig. 15, which represents the appearance of one of my specimens of *Chondrosteus*, is also interesting, because it shows two small elements lying in the specimen rather in front of, though in the same plane as, the pterygoid, which are most plausibly interpreted as reduced palatine bones. These occur also in the specimen which I have already figured. The figure also shows the parasphenoid more completely than it has yet been described; the most interesting feature is the extreme posterior extension of the bone, which runs backwards below the occipital region of the neural cranium and terminates in a notched posterior border. This notch must represent the posterior end of an aortic canal, which anteriorly is completely underlain by the parasphenoid until it divides into two, which open to the exterior through common carotid foramina, just as they do in Palæoniscids in general. From these carotid foramina deep grooves pass forward on the lower surface of the bone which represent the posterior part of the circulus cephalicus.

Some distance in front of the openings of the carotid foramina the bone widens to form a pair of ascending processes, which pass outwards and upwards below the prootic. Behind the process there is a notch which presumably transmitted the external carotid artery. Anteriorly the parasphenoid forms a somewhat broad pointed processus cultriformis, whose lower surface is flattened. The whole bone differs from that of the Carboniferous Palæoniscids in the same way, though to a greater extent, than does that of *Birgeria*. It agrees in its general morphology rather strikingly with the corresponding bone of *Saurichthys* as Stensiö described it, and is similar in its main features to the corresponding bone of *Gyrosteus* described by Smith Woodward, and is, as a whole, remarkably similar to *Acipenser* itself. At the same time this new specimen shows certain features—for example, the deepened hinder end of the maxilla and the depressed area on the outer surface of the lower jaw into which it was received, which are most reminiscent of Palæoniscids, and add to the certainty of the derivation of the Sturgeons from that group.

The preceding paper is to be regarded as an appendix to my former account of Palæoniscid structure and as a necessary preliminary to a future paper dealing with the structure of certain Mesozoic Ganoids. As the latter paper may not be completed for some time, I think it useful to publish these observations independently.

LIST OF LITERATURE.

HENNIG, E. 1925. 'Palæontographica,' vol. lxvii. pp. 115–133.

HERRICK, C. J. 1899. Journ. Comp. Neurology, vol. ix. pp. 157–455.

STENSIO, E. A. 1921. Triassic Fishes from Spitzbergen. Vienna, 1921.

TRAQUAIR, R. H. 1880. Trans. Roy. Soc. Edin. vol. xxix. pp. 343-391.

WATSON, D. M. S. 1925. Proc. Zool. Soc. 1925, pp. 815–870.

WOODWARD, A. S. 1898. Proc. York. Geol. & Poly. Soc. vol. xiii. pp. 461–472.

4. Notes on East African Birds (chiefly Nesting-habits and Stomach-contents) collected in 1926. By Arthur Loveridge, C.M.Z.S.

[Received August 5, 1927: Read November 15, 1927.]

The following observations were made while the writer was engaged on a comparative study of the herpetological faunæ of the Uluguru and Usambara Mountains in Tanganyika Territory on behalf of the Museum of Comparative Zoology, Cambridge, Mass. To these have been added half a dozen earlier unpublished notes.

With the exception of Dar es Salaam, Kilosa, Kimamba, Suna, and Sagayo, all localities mentioned are situated in one or other of these mountain-ranges, their approximate altitudes being as follows:-

Uluguru Mountains.		Usambara Mountains.	
Bagilo,	5000 feet.	Amani,	3000 feet.
Mkangazi,	3000 ,,	Bumbuli,	2000 ,,
Mkarazi,	1500 ,,	Kizerui,	4000 ,,
Nyange,	2500 ,,	Lushoto,	5000 ,,
Nyingwa,	7500 ,,	Lutindi,	4000 ,,
Vituri,	2000 ,,	Phillipshof,	5500 ,,

The nests of at least two of the birds mentioned are described for the first time.

My grateful thanks are due to Mr. Outram Bangs for determining half a dozen of the birds and confirming or correcting the other identifications made in the field, and to Drs. Chapin and Friedmann for naming the *Stephanoaëtus* and *Cinnyris m. usambaricus* respectively; also to Dr. Bequaert for determining hippoboscid flies, and Mr. Nathan Banks the ticks in stomach of *Buphaga*.

FALCO TINNUNCULUS CARLO (Hartert & Neumann).

Kestrels are known as *kipozi* in Kikami and *mesenga* in Kisumbara.

Observing one of these birds drop down and pick a lizard off a rock, the bird was shot, and a gecko (*Hemidactylus mabouia*) was found in its crop as well as a skink (*Mabuya striata*) in its stomach (Mkangazi, 20. x. 1926).

STEPHANOAËTUS CORONATUS (Linnæus).

On several occasions one of these birds was observed in the neighbourhood of the camp, but always chose to perch on the top of the higher trees well out of gunshot range. On the 27th my wife reported having found the nest, and watched the old bird apparently feeding a fledgling. The nest was built at a height of a hundred feet from the ground, near the top of a tree whose smooth and slippery stem had not a single branch for the first sixty feet from the ground. The tree was growing beside a stream which meandered along a well-wooded ravine. By climbing the steep hillside one was able to see partially into the nest, and was puzzled as to whether the bird it contained was adult or young. To day we returned armed with the forest officer's permission to cut down the tree if necessary, but as we approached the bird flew off and I shot it on the wing. It proved to be a young one (Phillipshof, 31. xii. 1926).

FALCO NAUMANNI NAUMANNI Fleischer.

A bird which I took to be a Lesser Kestrel, and known as *kitema* to the Wakami, had a brood of nestlings in an ideal site—a hole in the cliff-face overhanging about thirty feet of smooth rock (Mkarazi, 21. x. 1926).

TURACUS HARTLAUBI (Fischer & Reichenow).

Hartlaub's lourie is known as *kuluvu* to the Wasumbara. On examining the stomach of one of these birds, it was found to contain many seeds of the fruit of what is probably *Conopharyngia holstii* (*Tabernæmontana*). I am indebted to Mr. D. K. S. Grant, Chief Conservator of Forests, Tanganyika Territory, for this identification. Several young birds only just out of the nests were seen during the week (Phillipshof, 21. xii. 1926).

BUCORVUS CAFER (Schlegel).

Some natives brought me a cock bird in fine condition which they alleged had caught its head in a tangle of grass, through which it had thrust it, in an attempt to reach a rat whose runway was beneath. This was possibly true, or perhaps it had been taken in a game snare, which, of course, they would hesitate to report. The following morning I fastened a long length of cotton rope to its leg and tethered it to a peg in the garden. Then I tossed it a House-Snake (*Boaëdon lineatus*), which it neatly seized by the back of the neck and flew off with till brought up suddenly by the rope, whereupon it dropped the snake. This happened three times, but finally, after crunching the snake's head in its bill, it swallowed the reptile (Kilosa, 8. viii. 1921).

A second bird was shot in a cotton shamba by my collector. Its stomach contained red locusts, grasshoppers, and a black field-cricket (Kimamba, 15. viii. 1921).

BYCANISTES CRISTATUS (Rüppell).

The Silvery-cheeked Hornbill is the *mhondomondo* of the Wakami, the *hondo* of the Wasumbara.

Though the stomachs of many were examined, only fruit was found in them, yet at Amani one Sunday afternoon my wife and

I observed one of these birds with either a rat or a lizard in its beak, probably the former, to judge by the way its tail whirled round and round as the bird chopped it with his bill and shifted it about. At Lutindi the Trumpeter-Hornbill (*Bycanistes buccinator*) was shot feeding with Silvery-cheeked Hornbills in the same fig-tree. At Phillipshof, where both species occurred, a pair of these birds were observed high in the air mobbing a large bird of prey which I have every reason to believe was a Crowned Hawk-Eagle. Wasumbara natives, if not Mohammedans, eat the flesh of both these hornbills. The Trumpeter-Hornbill they call *kiungai*.

LOPHOCEROS MELANOLEUCOS (Lichtenstein).

The Crowned Hornbill is called *luhoya* in Kikami, *nkwembe* in Kisumbara.

The stomach of one of these birds held two round red fruits, a green mantis, a large caterpillar, and many green cetonid beetles. Another held a mass of beetle-remains; one of the species represented appeared to be a rhinoceros-horn. There were also several cetonids with white spots on their elytra (Amani, 3.xii. 1926).

HALCYON ALBIVENTRIS ORIENTALIS Peters.

The Oriental Brown-hooded Kingfisher is called *mndilila* in Kikami, *Kumbulu* in Kisumbara.

A native child conducted me to a circular well-like hole some ten feet deep and four feet in diameter in which he had seen a snake. The hole was close to the back-yard of a hut.

As we approached I saw a pair of Kingfishers on the lower branches of a young coconut-palm, and, thinking to secure both with one shot, took aim; before I fired, however, the hen flew off to another tree, but I secured both. In one was a black field-cricket, in the other several long wire-worm-like yellow beetle-larvæ. (The stomach of a bird shot at Kilosa, 4.i. 1921, held grasshoppers.)

Meanwhile my native collector, Salimu, had been capturing frogs in the hole, and was about to climb out when he found a Kingfisher's burrow about a foot and a half below the surface of the ground. I gave him my stick to measure the length of the burrow, and we ascertained that it went back to a depth of between three and four feet. Laying the stick on the ground in the same general direction taken by the passage, we sunk a shaft from above and came directly upon four white eggs (measuring 25×23 mm.) laid on a small collection of very finely-broken mollusk shells and coleoptera elytra, among which a large purple carabid wing-case was very conspicuous (Dar es Salaam, 6.xi. 1926).

MELITTOPHAGUS LAFRESNAYII OREOBATES Sharpe.

The Elgon Cinnamon-chested Bee-eater is called *kinega* by the Wakami.

A nest in a hole in a bank was found to contain three pure white eggs measuring 22×18 mm. They were on the point of hatching. Both parent birds collected (Phillipshof, 20. xii. 1926).

Of three nests examined to-day one contained three fresh eggs; a second three well-incubated eggs apparently laid at considerable intervals, one of which was addled, the shell being minutely punctured, presumably by the claw of one of the parent birds; in the third nest were three young birds almost ready to fly. The nests consist of a pile of fly and beetle wings and are situated about two to two and a half feet from the entrance of the burrow, the latter taking a sharp turn just before the nest-chamber. The eggs are generally much stained with the reddish soil (Phillipshof, 21. xii. 1926).

One nest with three very slightly-incubated eggs and a second containing an egg and two recently-hatched young (Phillipshof, 30. xii. 1926).

MEROPS APIASTER APIASTER Linnæus.

I saw a flock of European Bee-eaters in poor plumage going south-east in short stages as they stopped to catch insects from time to time in the early morning sunshine (Vituri, 27. x. 1926).

CORACIAS NEAVIUS NEAVIUS Daudin.

This bird is called *Lohoyu* in Kinyaturu; in the stomach of a hen bird just killed there was a lizard (*Agama hispida distanti*) (Suna, 3. x. 22). Very large grasshoppers in the stomach of a cock bird (Shanwa, 20. x 22).

CAPRIMULUGUS EUROPÆUS MERIDIONALIS Hartert.

The stomach of a male Nightjar shot to-day was full of termites Kilosa, 4. ii. 21).

RIPARIA FULIGULA RUFIGULA Fischer & Reichenow.

The Brown-throated Rock-Martin is called *sangalala* in both Kikami and Kiluguru, while in Kisumbara it is *kizelele*.

A nest, containing young, was seen affixed to a rock-face at a height of ten feet from the ground (Bagilo, 23. ix. 1926).

Watched a parent bird feeding a nestling which was crouching on a very narrow ledge of rock some six feet from the ground. How it reached this position is something of a mystery, for the rock was in the centre of a large ploughed field and the nestling apparently too young to fly. There was no trace of a nest on the rock, which was about twenty feet long and twelve feet in height. A cliff, where the nest was probably located, was quite a hundred yards away (Nyange, 9. x. 1926).

Three young, in a nest over the door of a room in the house we are temporarily occupying, flew to-day, but returned to the nest to sleep this evening (Bumbuli, 15. xii. 1926).

PSALIDPROCNE HOLOMELÆNA MASSAICA Neumann.

This martin, or bank-swallow, is known to the Wakami and Wauluguru by the same name as they employ for the preceding species. The Wasumbara apply a diminutive to their name for the Brown-throated Rock-Martin and call it *kizelele kidogo*.

Shot several of these martins, which are very numerous here. Two of them harboured hippoboscid flies (*Ornithomyia fur* Schiner) among their feathers (Bagilo, 23. ix. 1926).

While walking up one of the terraced paths of the arboretum, I halted to speak to a native, and thus alarmed a bank-swallow, which burst from its nest-hole in the cutting beside me. Two young ones which were able to fly were found in the nest-chamber, which was situated a foot from the entrance (Amani, 24. xi. 1926).

Two pure white eggs (measuring 19 × 13 mm.) were taken from a nest composed of various kinds of lichen situated in a burrow in a bank forming a cutting on one side of the terraced roadway. The nest was approximately 90 mm. in diameter. Both parent birds were shot (Phillipshof, 21. xii. 1926).

A second nest, containing two very slightly-incubated eggs, was found; a third with two eggs almost ready to hatch; a fourth with two fledglings nearly ready to fly. Both the latter were in burrows only a foot above the ground; the nest-chambers were about two feet from the entrances. Nests from which sitting birds were disturbed invariably held hippoboscids often so gorged with blood as to be unwilling to move (Phillipshof, 22. xii. 1926).

A fifth nest found to-day held two very slightly-incubated eggs. A bird was seen flying to a burrow with a long wisp of lichen, three times its own length, in its bill. Other nests in process of construction were found, and one, from which the young had recently flown, held eight bloated hippoboscids (Phillipshof, 30. xii. 1926).

ALSEONAX SUBADUSTA Shelley.

A nest was found by my wife upon a horizontal lichen-clad bough of a tree growing on the outskirts of the forest; the situation chosen was about six feet from the ground. Externally the nest was composed of grey lichen identical with that which covered the whole tree; internally it was beautifully lined with down and feathers. The outside measurements were 95 × 65 mm.; inside it measured 40 × 25 mm. The three eggs were uniformly bluish-grey, and contained embryos so large that it was impossible to preserve the eggs (Phillipshof, 31. xii. 1926).

TCHITREA PERSPICILLATA SUAHELICA Reichenow.

The Grey-breasted Paradise Flycatcher is the *nyalumbizi* of the Wakami, the *talalamzitu* of the Wasumbara.

A cock bird was shot from a nest built in the triple fork of a shrub at the forest-edge. The nest measured 80 mm. outside diameter and 55 mm. inside. The outside depth was 65 mm. and the inside about 35 mm. The nest was a very beautiful structure of green moss held together by spider webbing, of which there were fleecy white masses here and there looking like tufts of raw cotton. The interior was lined with shredded fibres, fine grasses, and rootlets. The eggs, three in number, were quite fresh. One measured was 19×15 mm. They are slightly buffy-white in ground-colour with a ring of reddish-brown, and a few purplish, spots around the larger pole. There are a very few flecks of the same on the rest of the egg.

In life the skin at the corner of the mouth, as well as the wattle-like expansion of skin around the eyes, is vivid Cambridge blue, but fades on preservation; in sharp contrast all the rest of the head-feathers, including the short crest, are dark metallic blue; the breast is smoky-grey, shading off into the white feathers of the under tail-coverts; the inner wing-coverts are also white. With its rufous back and tail (the elongated plumes in the latter measure eleven inches in length, or nearly four times the length of the bird itself) one can but imagine what a beautiful sight a cock flycatcher sitting on its moss-green nest makes (Phillipshof, 21. xii. 1926).

A hen bird was found sitting on another nest holding two eggs, but these were not collected (Phillipshof. 30. xii. 1926).

LANIUS COLLARIS HUMERALIS Stanley.

The hen was shot from a nest which measured approximately 140×110 mm. externally, while the inner cup was 70 mm. in diameter and 45 mm. deep. Neatly and strongly constructed of very fine twigs and lichen outside; lined with grasses and very fine rootlets. One of the two eggs was well-incubated, the other apparently addled. One measured 22×17 mm., was white in ground-colour and speckled with brown and purplish, but chiefly grouped in a small band around the larger pole (Phillipshof, 23. xii. 1926).

DICRURUS LUDWIGI LUDWIGI Smith.

Ludwig's Drongo is known as *miamba* to both Wakami and Wasumbara, but the name is probably applied to all drongos.

I saw a White-necked Raven (*Corvultur albicollis*) sitting quietly on the branch of a fir-tree, when my approach disturbed it. As it dived off valleywards a pair of drongos, hitherto unnoticed, pursued it, and one of them actually rode on the rump of the larger bird as it pecked it mercilessly. This was on the 18th, and I witnessed a similar attack to-day (Amani, 24. xi. 1926).

CORVUS ALBUS P. L. S. Muller.

The White-bellied Crow is called *kinzulenzule* in Kikami, *konguru kidogo* in Kisumbara.

A pair of adult birds were feeding a fledgling in the tops of the eucalyptus-trees in the hotel grounds. Being requested to shoot them on account of their depredations, I found the food to be a two-horned chameleon (*Chamæleo fischeri multituberculatus*) (Lushoto, 20. xii. 1926).

CORVULTUR ALBICOLLIS Latham.

The White-necked Raven is known to the Wakami as *bondwa*. while the Wasumbara call it *konguru kubwa*.

Stomach-contents consisted of frogs recognizable by their bones. See note under *Dicrurus* also (Amani, 22. xi. 1926).

BUPHAGA ERYTHRORHYNCHA Stanley.

The Red-billed Oxpecker is called *shashe* by the Wasumbara, it has no name in Kikami as it does not occur in their district.

A pair of these birds were shot off the backs of cattle, and on examination of their stomachs only one was found to contain ticks (*Amblyomma*, sp. nymph., *Ixodes pilosus* Koch, and *Rhipicephalus punctatissimus* Gerst.?), though both held a great deal of hair and blood (Phillipshof, 27. xii. 1926).

ANDROPADUS MASUKENSIS ROEHLI Reichenow.

This Bulbul is known as *pundwe* in Kikami.

A nest was found five feet from the ground in a sapling in open forest near the top of the mountain, *i.e.* about 1400 metres. The nest, which measured 3 × 3½ inches, was slung in a fork; it was made of fibre and rootlets and lined with finer black fibres, very much like horsehair; there is a little moss on the edges of the nest where it was attached to the branches. The two eggs, already well incubated, measured 25 × 16 mm., and were pinkish-white in ground-colour heavily blotched with brown and black (Mt. Lutindi, 10. xii. 1926).

ARIZELOCICHLA NIGRICEPS (Shelley).

A nest had been built upon some bramble-sprays which were growing from the top of a bank bordering the road; thus the nest was only five feet from the ground, though quite eight feet above the road-level. Externally this nest was composed of tendrils and coarse grass-stalks, internally it was lined with fine grasses. Outside it measured 130 × 55 mm.; inside 70 × 30 mm. The second of the two eggs was only laid to-day; in all probability a full clutch would consist of three eggs. These measured 25 × 6 mm., were pinkish-white in ground-colour, but this was so heavily overlaid with brown and purplish mottling as to be almost obscured. The hen bird was collected together with the nest and eggs (Phillipshof, 31. xii. 1926).

CINNYRIS LOVERIDGEI Hartert.

This, as well as other sunbirds, is called *kisozi* by the Wakami. I have not found the species in the Usambara Mtns.

A nest was found to-day hanging from, or rather among, a long fringe of exquisite moss, which trailed over a low cliff (rock) in the rain-forest; it was some nine feet from the ground. In length the nest measured seven inches and in breadth four. Externally it is composed of still living green moss, with a few fronds of fine fern besides some dead and skeleton leaves. The structure is apparently lined with the finest rootlets, and then again with the finest and most hair-like grass, so that at first sight it seems to be lined with hair. The beautiful little nest so harmonised with its surroundings that it was very difficult to locate if once you looked away from it (Bagilo, 23.ix.1926).

A hen bird was observed building on the end of a branch of a tree in the rain-forest. The nest was situated quite thirty feet from the ground and was nearing completion (Nyange, 6.x.1926).

A series of skins as well as another nest were collected here, where the bird is quite common. The record extends its known range to the southward somewhat, and its altitudinal habitat would appear to be 2500 to 7500 feet (Nyingwa, 18.x.1926).

Cinnyris obscura neglecta Neumann.

Kizozi in Kikami, *mzozi* in Kisumbara, *chozi* in Kiswahili, but probably none of them specific but embracing all sunbirds.

A hen was shot off a nest (measuring 160 × 70 mm. over all) attached to creepers projecting from a rock, so that the nest overhung a path in the rain-forest, and was seven feet from the ground. The nest is composed of dead and skeletonised leaves together with fibres of desiccated grasses; the interior is neatly lined with silky seed down. The whole structure strongly resembled a fortuitous assemblage of dead leaves similar to several clumps in the same creeper. The two eggs measured 18 × 12 mm., and were dull or faintly bluish-white in ground-colour, heavily blotched and scribbled with purplish-brown; these markings were concentrated in a circle around the larger pole, as well as being scattered over the whole surface. The eggs were very slightly incubated (Amani, 29.xi.1926).

Cinnyris mediocris usambaricus Grote.

Native names as in last species.

A cock bird was shot from a nest (measuring 170 × 100 mm. over all) which was attached to the terminal sprays of a high bramble-bush, so that the nest was nine feet from the ground. Externally it was constructed of dry grass with a very little moss, internally felted with a thick layer of vegetable silk and a single white fowl feather at the entrance-hole. The hen was twice flushed (on 21st and 22nd) from a single well-incubated egg; the latter measured 16 × 11 mm., and though the ground-colour was in reality whitish, it was so heavily overlain with chocolate that it was almost entirely obscured (Phillipshof, 22.xii.1926).

A second nest (measuring 200 × 100 mm. over all) was situated in a thorny shrub at a height of six feet from the ground. Structurally it agreed with the first but for the presence of several birds' feathers at the entrance. Both the cock and hen bird were shot from the nest, which held two very slightly-incubated eggs strikingly different from each other as well as from the egg found yesterday. One of these eggs had a greenish-white ground-colour, well streaked with brown and encircled with purplish-brown around the larger pole. The second egg was pale fawn or pinkish-fawn, scantily speckled or streaked with darker (Phillipshof, 23. xii. 1926).

POGONOCICHLA CUCULLATA ORIENTALIS Fischer & Reichenow.

A hen of the Coastal Yellow-breasted Forest-Chat was shot from a nest practically upon the ground against a stump which was itself certainly not more than eighteen inches high. Leaves, which also carpeted the forest-floor round about, had drifted against the stump until the nest was so marvellously like its background that it would have been impossible to detect it had not the bird left it. This nest measured some 150 mm. in diameter, and was very loosely constructed of dry grass with dead leaves and a little moss adhering to the grass; internally it was lined, at the bottom only, with a little vegetable down and a feather or two. The entrance was on the side. There were two eggs in the clutch, both of which held embryos and measured 21 × 14 mm. While one egg was greenish-white in ground-colour the other was buffy-white; both had the upper pole heavily marked with reddish-brown, and some flecks and spots of the same colour were scattered sparsely over the rest of the surface. The nest and eggs showed a strong resemblance to those of the British Robin, a near relative of this chat, though the situation was such as a Willow-Warbler would have selected (Phillipshof, 28. xii. 1926).

5. Report on the Deaths occurring in the Society's Gardens during the Year 1927. By H. HAROLD SCOTT, M.D., F.R.C.P.Lond., D.P.H., D.T.M. & H.Camb., F.R.S.Ed., F.Z.S., Milner Research Fellow in Comparative Pathology, London School of Hygiene and Tropical Medicine; Pathologist to the Society.

[Received February 1, 1928: Read March 6, 1928.]

It is gratifying to be able to report that again there has been a slight decrease in the number of animals coming to autopsy. In 1925 there was a reduction of 9 per cent. on the figures for 1924; in 1926 just over another 4 per cent.; and during 1927 the total was 1037, as compared with 1150 for the preceding twelve months, a 9-per-cent. decrease.

The monthly distribution in the various groups of Mammalia, Aves, and Reptilia is given in Table I.

TABLE I.—Showing the Distribution month by month of Animals submitted to Autopsy during 1927.

Month.	Mammalia.	Aves.	Reptilia.	Total.
January	22	43	28	93
February	20	41	17	78
March	12	35	13	60
April	15	35	18	68
May	13	30	20	63
June	20	35	12	67
July	38	35	49	122
August	14	31	47	92
September	28	29	31	88
October	23	41	24	88
November	19	53	17	89
December	54	66	9	129
Total	278	474	285	1037

As in my previous reports, for purpose of comparison a separate Table (Table II.) is given to show the total number and the monthly distribution of those animals which die within six months of arrival in the Gardens. This amounts to 424, practically the same as in 1926 (425), but with the smaller total of all deaths implies a higher percentage, namely 40·88 as compared with 36·95 in 1926. These, however, must be interpreted in conjunction with the figures of the whole number of new arrivals, a matter outside the scope of my report.

TABLE II.—Showing the Distribution month by month of those dying within 6 months of arrival.

Month.	Mammalia.	Aves.	Reptilia.	Total.
January	8	10	13	31
February	6	11	7	24
March	7	7	9	23
April	2	11	11	24
May	—	6	13	19
June	15	9	7	31
July	25	8	34	67
August	9	13	36	58
September	9	7	23	39
October	8	17	15	40
November	4	15	11	30
December	19	16	3	38
Total	112	130	182	424

Perhaps the best method, from the pathological point of view, of gauging the health of animals in the Gardens is the presence or absence of disease of an epidemic or communicable nature. During 1927 there has, fortunately, been no outbreak of an epidemic nature. This is certainly a matter for congratulation of those in charge of the welfare and hygiene of the animals. Table III. gives the number of cases of communicable disease examined at the Prosectorium.

I would beg particularly to call attention to the fact that Anthrax this year has spared the Gardens altogether, and that Nocardiosis, which was responsible for 15 deaths among the Kangaroos in 1925 and 3 in 1926, has also been absent. This is a matter for jubilation and thankfulness, but not for complacence, for this is a disease which may disappear for several years and then crop up suddenly again in a manner as yet unexplained, as was mentioned in the special communication to the Society in 1925 *.

---

* "A Streptothrix Disease of Wallabies," P. Z. S. 1925, ii. pp. 799–818.

TABLE III.—Giving the number of Cases of the Important Communicable and Preventable Diseases during the Year 1927.

(The figures for the previous year are given for comparison.)

Disease.	Mammalia.		Aves.		Reptilia.		Total.	
	1927.	1926.	1927.	1926.	1927.	1926.	1927.	1926.
Tuberculosis	13	38	12	13	3	3	28	54
Tuberculosis and Mycosis	—	11	17	19	—	—	17	30
Mycosis	3	8	27*	48	1	9	31	65
"Enteritis" ...	20	20	32	82	25	26	77	128
Rickets and allied conditions (Osteomalacia, Osteoporosis, Osteitis fibrosa, etc.).	19†	12	6	10	1	1	26	23
Pulmonary :—								
Capillary Bronchitis	14	16	14	27	16	25	44	68
Lobar Pneumonia	3	6	18	10	7	11	28	27

* In six others Mycosis was present, but in an early stage, and took little if any share in causing death.

† In three others there were signs of old rickets, and death was due to other causes.

1. *Tuberculosis.*

The number of cases of this infection was largely swelled in 1926 owing to an epidemic in the Monkey House. This year there has been no epidemic, and the total has again fallen; it is satisfactory to be able to state that the figure for mammalian cases is considerably lower than in 1925, before the outbreak.

The 13 mammalian cases were:—

Two Axis Deer, two Virginian Deer, a White-bearded Gnu, an Abbott's Duiker, a Waterbuck, a Thar, a Grey Mongoose, a Rhesus Macaque, a Humbolt's Woolly Monkey, a Hamadryas Baboon, and a Kangaroo.

Some of these presented the usual typical lesions, and need not be referred to in detail. Suffice it to say, that in three of the four Deer the infection was respiratory in origin and in an advanced stage in the lungs, but in none were any "perles" present. In one of the Virginian Deer (D.B. No. 879/27) the disease had entered by the alimentary route. The animal had been born in the Gardens and was 18 months old. Tuberculous ulceration was present at the lowest part of the small intestine, but the cæcum and the large intestine were much more severely involved. In the colon there were large ulcers, three of them extending almost completely round the lumen, while at the junction of the small and large bowel was to be seen an excellent example of the uncommon condition of a thick caseated collar of tuberculous deposit. The lungs had been invaded secondarily by way of the pulmonary circulation, so that both these organs contained scattered miliary lesions.

In well-marked contrast to these were a White-bearded Gnu (No. 456/27) and the Waterbuck (809/27). The former, *Connochætes albojubatus*, was 8 years of age and had been born in the Gardens. The only symptom noticed was that it had seemed to be getting thinner during the two or three weeks preceding death. There were numerous "perles" on the serous membranes, and calcareous masses in the liver, spleen, and some of the lymphatic glands. It is certainly a matter for wonder that the animal lived so long. There was hardly any recognizable lung-tissue left, each organ being largely converted into a vast, hard, board-like caseated mass breaking down here and there to the formation of cavities. The pericardium also contained many hard, caseated, and calcareous nodules.

The condition found in the Waterbuck closely simulated the last. The pleuræ were adherent and presented "perles" in enormous numbers; all three lobes of the right lung and the upper lobe of the left contained hard caseated and cretaceous masses, but none actually calcified; the lower lobe of the left lung was softening and breaking down to the formation of cavities. In spite of the advanced state of the disease in the lungs, no other viscus was found to be involved. This animal had given birth, 36 hours previously, to a slightly premature calf. Examination of the latter revealed no macroscopic evidence of tuberculous infection.

The case of the Thar, *Hemitragus jemlaicus*, No. 641/27, was of great pathological interest. It had been more than 11 years in the Gardens, and had presented no symptoms until the morning of its death, when it was noticed to be suffering from marked respiratory distress, and died whilst it was being conveyed to the Sanatorium. It was believed to be an old animal, and had at one time or another fought and overcome all the other males on the Mappin Terrace, where it reigned supreme and ruled by terror. At the *post-mortem* examination the lungs were seen to be œdematous and ballooned, petechiæ were present on the pleural surfaces, there were weak pleuro-pericardial adhesions on the left side, and about 1500 c.c. of clear amber-coloured fluid in each pleural cavity. In the pericardial cavity was 500 c.c. of similarly coloured fluid, but it coagulated partly on standing. There was very marked atheroma, not only of the aortic arch, but also extending down the thoracic aorta, and the aortic valves were calcareous. There was atheroma of the pulmonary aorta also, but to a less degree. At the base of the septal cusp of the systemic aorta, in the membranous part of the interventricular septum, was an opening 1 cm. in diameter with a hard, calcified edge, and allowing free communication between the ventricles. As regards other organs, the liver and kidneys were tough and fibrotic, as was also the spleen, but in the last were hæmorrhagic areas resembling infarcts. Portions of the lungs, liver, kidneys, and spleen were taken for microscopical examination, and it was a matter of considerable surprise to find tubercles with giant-cell systems and bacilli in considerable numbers in the lungs and the spleen, fewer bacilli in the kidney, where the giant-cells were much in evidence, but none in the liver.

This case is of particular interest for three reasons:—1. Congenital cardiac defects are believed to be rare in animals (this point is again dealt with subsequently), and this one, with a serious lesion, had not only lived in apparently excellent health for many years, but had more than held its own in the battle of life. 2. The existence of tuberculous disease, although it proved to be fairly widespread, was quite unsuspected, even when the *post-mortem* examination was made. 3. The existence of tuberculosis together with congenital cardiac mischief is very rare.

Another case of more than passing interest was that of a Kangaroo Island Kangaroo, *Macropus fuliginosus*, No. 654/27. Tuberculosis is far from common in these marsupials, and it is intended that a fuller account will be given elsewhere; but a few remarks may be made here. The lungs showed a few miliary tubercles; old pleural adhesions were present on both sides, and pleuro-pericardial on the left. The axillary glands on the right side were swollen and full of creamy or cheesy pus, and one was adherent to the capsule of the shoulder-joint, which itself was the site of a tuberculous pyarthrosis. There was a large glandular mass at the root of the neck on the left side of the trachea, as large as a tennis-ball, and this mass had broken down to form an abscess, while the cervical glands above it were enlarged and purulent. The iliac and lumbar glands were enlarged and caseated, as were also those along the abdominal aorta, and there was a caseated adherent aggregation of glands at the cœliac axis. The thoracic duct was stuffed with caseous pus. Finally, there were tuberculous abscesses in both sterno-clavicular joints.

The culminating point of interest is that portions of tissues were sent to Dr. Stanley Griffith, who has written to say that the type of tubercle bacillus was the *avian*.

Three cases among the monkeys were of sufficient interest to warrant mention in a little more detail. The first of these was a Rhesus Macaque, No. 166/27. The primary portal of entry was respiratory, there being a condition of bronchopneumonic phthisis of both lungs, to a greater degree in the right. Thence the infection had spread to the pleuræ and by the lymphatics accompanying the internal mammary artery to the infra-clavicular glands. These had in due time become caseated, and, from the blockage thereby occasioned, backflow had occurred to the inferior surface of the diaphragm and the falciform ligament of the liver. Generalization at a later period by way of the blood-stream had led to invasion of the viscera—kidneys, spleen, liver, mesentery, left Fallopian tube, and the right cerebral hemisphere, where there was a small caseated focus, 0·5 cm. in diameter, in the posterior Rolandic gyrus. The pericardium also was thickened and tuberculous, and beneath it milia were seen in the myocardium. The mesenteric tubercles were all very small and lay along the vessels, and those beneath the diaphragm were situated along the termination of the superior epigastric and the inferior phrenic arteries. It is important to note that the intestine itself was not affected, nor the mesenteric glands, the invasion of the peritoneum, mesentery, and abdominal viscera being vascular in origin.

The second was a Humbolt's Woolly Monkey, No. 705/27, which, however, did not contract the disease in the Gardens, since it died with widespread and severe lesions less than a fortnight after arrival. The lungs were heavily infected with milia, while the lower lobe of the left was solid and caseated. There were numerous tuberculous ulcers in the small intestine and a general infection of the peritoneum and invasion of the liver, spleen, and kidneys. The mediastinal glands were matted and caseated, and the abdominal glands presented a condition known in the human subject as *Tabes mesenterica*.

The third was a Hamadryas Baboon, and is worth recording because of the character and distribution of the lesions, and because this is the first of these animals dying from this disease within my experience. It was a female which had been in the Gardens for nearly six months, but fortunately had not been transferred from the Sanatorium to the Monkey Hill, or there is good reason to fear we might have had a devastating epidemic to record. The lesions were peculiarly distributed. Both lungs were studded fairly thickly with milia, while the pleuræ were uninvolved. The intestines were free from disease, but the omentum was dotted over with milia, as was also the mesentery, the tubercles in the latter being more densely disposed along the course of the vessels. The liver, spleen, and kidneys were studded with small tubercles, scattered throughout in the two former organs, but confined to the cortical regions in the last. Sparse tubercles were present on the external aspect of the urinary bladder, none in the interior; they were seen also on the anterior and superior surfaces of the uterus and in the left broad ligament. The bladder, uterus, and broad ligament were almost certainly infected by contiguity from the peritoneal tubercles.

The cervical and axillary glands on both sides were affected; they were enlarged, boggy, and broken down, to become, as it were, mere sacs of pus, while one of the axillary on the right side had adhered to the capsule of the shoulder-joint and opened into the joint itself. Both sterno-clavicular junctions were bathed in creamy tuberculous pus, possibly from infection of the infra-clavicular glands, and these two had united above so that the top of the sternum itself was also bathed in similar pus. The tonsils were quite healthy, and the cervical adenitis had not arisen from infection there. Within the skull a caseous focus was found in the meninges lining the bone over the left post-Rolandic area, measuring 1·4 × 0·9 cm., and indenting by pressure the cerebrum beneath, although no tubercles were found elsewhere in the brain or meninges.

Of the Avian cases there is not much to note. Most of them showed typical lesions, but the following four exhibited peculiarities worthy of brief mention:—

The first two were Hybrid Burmese and Black-winged Peafowls, *Pavo muticus* × *Pavo nigripennis*. Both were bred in the Gardens and hatched the same day, August 22nd, 1923. The first died on April 26th, 1927, the second on October 3rd. The first had for a fortnight or so preceding its death showed signs of difficulty in breathing, and had held its head extended, with obvious respiratory distress, after the manner of a bird infected with Syngamus (Gapes); in fact, this was believed to be the cause. At the autopsy, there was found, 3 inches above the level of the entrance of the trachea into the thorax, a granular tuberculous mass the size of a large pea, which acted like a ball-valve and practically blocked the lumen of the trachea; it had infiltrated the wall of the trachea and could be seen from the outside of the tube. There was no Syngamus. The lungs were not affected. There was, however, tuberculosis of the alimentary tract, also somewhat anomalous in character. In the upper part of the duodenum was a nodular mass as large as a walnut, yellowish-grey in colour, infiltrating and extending through to the serous aspect; just above this were two smaller deposits the size of peas. In each cæcum was a caseated tuberculous mass as large as a cob-nut, and in the left a second nodule a little smaller. The liver and spleen contained miliary tubercles, sparse in the former and small, more numerous and rather larger in the latter.

In the second Peafowl the disease was again strangely distributed. There were three tuberculous ulcers, the largest, measuring 2 cm. in diameter, being found in the duodenum; the other two, 1·5 and 1·0 cm. respectively, in the lower ileum. Small tubercles were visible on the serous aspect of these ulcers. In the spleen there were numerous deposits, but none larger than hempseed; in the liver they varied from milia to the size of a small cherry. In the head of the pancreas was a tuberculous deposit. The only other site found involved was the thyroid gland. Both lobes of this were much enlarged, appearing like walnuts, the right measuring 4 × 2·5 cm. and the left 3·8 × 2·2 cm.; each was made up of closely-aggregated grey-white deposits.

A third case was an All-green Parrakeet, *Brotogerys tirica*, No. 941/27, which had been in the Gardens for over 13 years. The intestine presented the form of tuberculosis in which nodules of deposit are present in the deeper layers of the wall, beneath the serous coat, but without ulceration. The liver contained a few bacilli; in the spleen the foci, though small, were numerous and bacilli very many. *Death* was due to lobar pneumonia; both lungs were of a dark purple colour, and each sank as a whole in water. In sections of the pulmonary tissue sparse tubercle bacilli were seen, but the pneumonic condition was not itself tuberculous.

Lastly, a Smew, *Mergus albellus*, No. 605/27, with a large tuberculous abscess of the pad of the right foot, with necrosis of middle phalanx. Careful search failed to discover any other focus of the disease, which had, therefore, probably been contracted by local inoculation of a wound. The tubercle bacilli were present in large numbers, but secondary contamination had arisen to produce the extensive cellulitis and the malodorous pus.

There have been three Reptilian cases during the year, and tuberculosis amongst such is sufficiently rare to merit detailed mention. It may be noted that in 1925 and in 1926 there were also three cases in each year.

In 1925 the cases were a Rough-eyed Cayman, *Caiman sclerops*, a Vivacious Snake, and Red Rattlesnake; in 1926 another Rough-eyed Cayman, an Æsculapian Snake, and a Mexican Black Iguana; in the year under review a Puff-Adder, an African Python, and a Gangetic Terrapin. Those for the first two years have already been spoken of in the respective annual reports.

The two snakes, Puff-Adder and Python, had undoubtedly brought the disease with them, for the latter had been in the Reptile House only 16 days and the former less than a month. In the case of the Python, *Python sebæ*, the disease was respiratory; there were numerous tubercles, each of the size of hemp-seed, scattered through the lung; there were a few minute deposits also in the liver, but none were found elsewhere. Tubercle bacilli were very numerous in sections of the lung-tissue.

The Puff-Adder showed two abscesses with purulent, not caseated, contents, situated in the subcutaneous and muscular tissues near the cloaca; there was, however, no connection between the abscess and the intestine, which was, in fact, quite healthy. The bones were not invaded, but the intercostal muscles were necrotic over the area involved.

The third, the Gangetic Terrapin, *Trionyx gangeticus*, No. 99/27, was brought over from Malay in June 1925 and died on February 3rd, 1927. The origin of the tuberculous infection in this case is a matter rather of conjecture. The viscera all appeared to be healthy. The plastron was perforated anteriorly to the right of the middle line, and there was another perforation in the membranous portion posteriorly on the same side. On removal of the plastron, the inner ends of both clavicles were seen to be necrosed, with erosion of 1–1·5 cm. of the shafts the whole being bathed in pus. Beneath the posterior perforation was another abscess in connection with the erosion of the right ilium. Whether the bacilli had entered by way of the eroded plastron, or whether there had been tuberculous affection of the bones or joints with the formation of abscesses which had made their way through from within, it would be difficult to say with certainty, for most terrapins show erosions of the plastron, and lodgement of organisms, *B. necrophorus*, *B. tuberculosis*, etc., could very easily occur. In this case the external diameter of the perforation was greater than the internal, and this is more in favour of the hypothesis of entry through a damaged plastron, while, on general grounds, if the disease started from within, there would be greater likelihood of widespread internal mischief than perforation of a hard plastron.

2. *Mycosis.*

There has been less than half the number of cases of mycotic infection as compared with 1926, and reference to Table III. will show that reduction has taken place in all classes. Among the Mammalia there have been but three, and all these were met with during the final quarter of the year. They were all Cercopitheques, but of different species, namely, a Mona, a Burnett's, and a Tantalus Cercopitheque. In only one of the three, the Burnett's Cercopitheque, was the mycotic infection the actual proximate cause of death.

The Mona Cercopitheque, No. 906/27, had been nearly two years in the Gardens. The actual cause of death was an ulcerative gastro-enteritis; the stomach showed many small discrete ulcers with inflamed borders, and in the large intestine there were others whose bases were occupied by sloughs. Mycotic invasion was evidenced by hard, yellow nodules, up to 7 mm. in diameter, in the spleen, and by larger numbers of quite small deposits in the liver, mostly miliary, some the size of a hempseed.

In the Tantalus Cercopitheque, No. 1007/27, which had been in the Gardens less than 3 months, the liver and spleen were again the organs chiefly involved. In this animal the foci generally were smaller, pin-point to millet seed, more numerous in the spleen. The mesenteric glands were also enlarged (in the Mona they were normal), and one was seen to be definitely caseating in places when opened, the others being swollen and congested only. No acid-fast bacilli were found in any of the lesions. There was also present a patchy bronchopneumonia, but death itself was due to a severe intestinal hæmorrhage. The lowest 8–10 inches of the small intestine were filled with fresh blood. The cause of this could not be discovered; the wall of the bowel was very congested and presented minute petechiæ, but no ulceration.

In the Burnett's Cercopitheque, No. 946/27, the distribution of the lesions was the same as in the last case, but they were of a more severe degree. The liver was studded fairly densely with small deposits, mostly miliary in size; in the spleen the foci were much larger, varying in size from 2 mm. to as much as 1 cm. in diameter. In the tail of the pancreas was a minute focal deposit measuring 1–2 mm., and several of the mesenteric glands were enlarged and congested, and when cut across, some of them were seen to contain minute deposits, pin-point to pin-head in size. No lesions were found elsewhere and no acid-fast bacilli were detected in any of the tissues, but from the spleen a pure culture of *Aspergillus fumigatus* was grown.

Amongst the Birds there have been 27 instances this year. This number does not include six in which the infection was in an early stage, limited in distribution, and took no share in causing death.

The lesions in the majority were typical and need not be recapitulated here. The portal of entry in the 27 referred to was respiratory in 18, alimentary in 7, and uncertain in 2. One of the last was a Brown-shouldered Hangnest, No. 328/27, in which there was a single small deposit in each lung, while the liver was studded thickly with focal deposits to the size of a pea, in places confluent. Statistics have shown that the liver is the organ most often involved in avian mycosis, and may be the only one.

The other case of doubtful mode of invasion was a Mitred Guineafowl, No. 854/27. In this there was a focal deposit in each lung, that in the right measuring 1·5 × 1·5 cm., that in the left a little less. In the intestine was a single ulcer over a mycotic deposit in the bowel wall; the liver was studded with foci, while in the spleen was a single focus, 0·5 cm. in diameter. The pulmonary lesions seem to be the more advanced, and the intestine may have been invaded secondarily to this, but it is unusual to find two isolated foci of practically the same age in different lungs. On the other hand, if the pulmonary infection was secondary to the intestinal, one would expect the lesions in the lungs to be much more generalized. There is, of course, the possibility of dual infection nearly simultaneously.

Certain of the mycotic cases are worthy of more detailed account.

(1) Firstly, there have been several Penguins dying from this infection. Some had, as far as could be ascertained, not been long in the country, and all six which died here had probably brought the disease with them, as the condition was in all in a very advanced stage. These birds would seem to be very susceptible to mycotic infection, analogous, perhaps, to the susceptibility to tuberculosis of the non-immunized native races in Man, which fall ready victims to the disease when they come into contact with tuberculous infection inseparable from civilization.

There have been four King-Penguins, a Gentoo, and a Rock-hopper Penguin. Only one has been as long as 8 months in the

Gardens, and two only 2 months. The findings of one are fairly typical of all and may be given as an example, the others differing in small degree only.

King Penguin, *Aptenodytes patagonica*, No. 272/27, nearly 3 months in the Gardens. The left lung was occupied by a vast solid mass of mycotic growth, no lung-tissue being recognizable to the naked eye; in the right lung were numerous deposits scattered generally through the parenchyma. The left posterior air-sac was lined throughout with growth, while the right posterior sac contained many small deposits, and there were small discrete foci in the anterior also. In other instances an air-sac might be entirely occupied by growth which formed, as it were, a cast of the cavity.

(2) A Common Peafowl, No. 766/27. Both the cæca were packed and distended with mycotic growth which had infiltrated the wall and infected the overlying peritoneum. The liver was heavily involved and was very friable, almost crumbly to the touch, and from this, by contiguous extension, the growth had invaded the inner aspect of the abdominal wall. The liver had ruptured, whether spontaneously or from some blow—a very slight one would have sufficed,—and death was caused by the resultant hæmorrhage.

(3) A Satin Bower-Bird, *Ptilonorhynchus violaceus*, No. 890/27, showed widespread respiratory invasion. The left anterior air-sac was lined by growth and the left posterior was filled by it as with a cast; there were focal deposits in the left lung and in the right posterior air-sac. By direct spread from the right posterior sac the peritoneum had become invaded. Death from this heavy invasion would probably have soon taken place, but this was forestalled by a rupture of the liver, 1 cm. in length at the antero-superior surface, with consequent fatal hæmorrhage. The organ itself was fatty and unduly friable.

(4) A Pied Grallina, *Grallina picata*, No. 783/27, presented somewhat peculiar lesions. The anterior air-sacs were lined almost throughout by mycotic deposits, although the lungs themselves and both posterior sacs were intact. The peritoneum had been attacked and the intestinal coils were matted together with caseating deposit. Lying in the abdomen, on the front of the right kidney, was a small lead-shot. Round this there had collected a focus of mycotic growth, or perhaps one should say growth appeared to have taken place round this as a nucleus.

The actual cause of death was a hæmorrhage into the pancreas; the gland was almost entirely occupied by so extensive a collection of blood that the gland-tissue itself was only just recognizable.

(5) Lastly, a Sooty Rail, *Limnopardalis rhytirhynchus*, No. 759/27. This bird had probably arrived here already infected, since it died with severe respiratory disease some three months later. All four air-sacs were lined throughout by a continuous sheet of mycotic growth; there were several deposits scattered in both lungs; the peritoneum showed widespread

invasion, probably by direct extension from the posterior air-sacs. Both kidneys were similarly covered, and from the latter the mycotic coating could be peeled off, leaving the organs themselves intact. There were extensive injuries to the head and neck; the bird's companions had administered the *coup-de-grâce* in the only way at their disposal.

It is satisfactory to note that there has been only one isolated instance of Reptilian mycotic infection, and that was seen in the early part of the year, before the migration to the new Reptile House.

This case was a Tigrine Frog, which showed an enlarged and tough liver, studded throughout with greyish translucent deposits, and the kidneys were fused together in the middle line (probably a congenital abnormality). To the left of this was a mass which was at first considered to be a neoplastic tumour, but when examined microscopically, proved to be the condition described in 1926 in a special communication at a Scientific Meeting of the Society, as *Monilia batrachea*, together with new growth (see p. 119).

Though found in Bull-Frogs, Black-spotted Toads, Square-marked Toads, American Toads, African Toads, Indian Toads, White's Tree-Frog, the Common Frog, and in Salamanders, this mould had not previously been recorded here from a Tigrine Frog.

3. *Tuberculosis* and *Mycosis*.

Instances of combined infection by both of these have been much less during 1927, as is shown in Table III. Whereas in the previous year there had been 11 cases among mammals and 19 among birds, this year there have been 17 avian and no mammalian cases.

Of these 17, there were thirteen in which the portal of entry appeared to have been alimentary, and only two definitely respiratory. In one of the others, though doubtful, the latter was the more probable. This was an Upland Goose, No. 53/27. Both lungs were dotted with miliary deposits, while in the lower part of the left was a larger, focal, lesion, the size of a small pea. Growth was present in both posterior air-sacs, in the left forming a thick lining to the whole cavity, in the right scattered foci beginning to coalesce. The intestine, liver, and spleen were intact, but lying on and loosely attached to the lower part of the gizzard was a large mass the size of a crown-piece, flat or slightly concave against the gizzard posteriorly, convex anteriorly. This consisted mainly of mycotic growth, but intermixed with a few acid-fast bacilli. I am unable to explain the origin of this focus.

The second case of uncertain portal of entry was a Carolina Duck, *Lampronessa sponsa*, No. 684/27. The liver and spleen were both studded thickly with mycotic deposits, and no tuberculous admixture could be detected in either of these organs. The lungs and air-sacs appeared to be quite healthy, but at the base of the "quacker" there was a caseous mass, the size of a cob-nut, containing harder cretaceous foci. This was mainly mycotic in nature, but a few tubercle bacilli were also found.

Two other instances are worthy of record: one as an example of the intensity of infection which may be present although the bird may be to all appearances in good health, the other to demonstrate the necessity or, we may say, advisability of examining conditions presumably mycotic for the presence of tuberculosis also.

The first was a Double-spurred Francolin, *Francolinus bicalcaratus*, No. 184/27. This bird had exhibited no symptoms of disease prior to its being found dead, nor was it at all emaciated. At the autopsy the left lung was found to be infiltrated with many yellowish mycotic nodules to the size of hempseed; the air-sacs on the left side, anterior and posterior, had thickened walls from growth of mycosis. The pericardium was thickened, opaque, and infiltrated with similar deposits. All along the intestine, on its serous aspect, at short intervals were scattered mycotic nodules to the size of a small pea, and the mesentery was also invaded. These lesions appeared to be mycotic, acid-fast bacilli not being found in the lung or air-sacs and very sparse in the intestinal foci. The liver was densely studded with yellowish nodules and also with innumerable minute grey milia. In the latter tubercle bacilli were found in enormous numbers, in some of the former none, in others a few. It seems a fair inference from this that the larger nodules were mycotic, whereas the minute grey milia were tuberculous, and that in some cases the latter coincided with the former. The spleen showed a condition similar to that of the liver, but the nodules were less numerous. The pancreas was pink and congested and contained several yellowish nodules in the interior; sections of this gland showed tubercle bacilli in considerable numbers, but not nearly so many as in the liver and spleen. In the left kidney there was a focal lesion which also showed the mixed infection.

Seeing that mycosis is a disease with a chronic course, while tuberculosis is rapid, and that in most (though, it is true, not in all) cases tuberculosis is associated with wasting, whereas in mycosis the nutrition is well maintained, and, thirdly, since mycosis produces little if any harmful toxin, death occurring in most cases of uncomplicated mycosis by mechanical effects or so extensive a growth as to interfere seriously with function, in the majority of cases the mycotic infection is the primary and the tubercle bacilli become implanted later. In the cases just recorded, it would certainly seem to be so, for in the lung and air-sacs, with extensive mycotic growth, there were no tubercle bacilli found, whereas in the liver, spleen, pancreas, and kidney they were present together with mycosis, and in the intestinal lesions the latter was severe but the bacilli few.

This point is worth stressing because in human pathology the sequence is usually, if not always, the reverse of this—a mould infection being found as a secondary invader of a tuberculous cavity, for example. in a phthisical subject.

Lastly, the case of a Glossy Ibis, *Plegadis falcinellus*, No. 674/27 This bird died in the Eastern Aviary after a stay of 13 months. Both posterior air-sacs were lined with mycotic deposit, the right anterior containing several discrete flakes, while the left anterior was filled with a complete cast of growth. In the right lung were a few small deposits, the left being free. The peritoneum was opaque, thickened, and covered by growth which had apparently spread from the adjacent posterior air-sacs. The spleen was also covered and the kidneys were in the same condition; the growth could be peeled off both these organs, and on section no invasion could be seen from the interior. *Aspergillus fumigatus* was grown from these lesions, and tuberculosis was not suspected until microscopical examination of sections of the tissues was made, when the bacilli were found to be present, but not in large numbers. There can be no doubt, I think, in this case that the tuberculosis was a secondary implantation on the mycotic site.

4. *Enteritis.*

This condition, or group of diseases, is responsible for more fatalities than any other single factor. The same is noted in all Zoological Gardens. During 1927 there has been a marked improvement in this respect as compared with the figures for recent years. From 165 recorded in 1925 there was a fall to 128 in 1926, while in 1927 there have been but 77—that is, a reduction of 23 per cent. and 40 per cent. respectively in each of the last two years on the figures of the year preceding.

Various organisms have been isolated during the year from cases of enteritis; and seeing that from several animals presenting similar symptoms and the same morbid appearances an organism was obtained, not only from the intestine, but also from the bile, the portal blood, and the spleen-pulp, which gave identical morphological, cultural, and fermenting reactions, it is probable that this was causative of the disease in question.

Thus, from a Serval, No. 208/27, three Scottish Wild Cats, Nos. 405, 409, and 410/27, and a Leopard, No. 430/27, a Gram-negative bacillus was isolated which was motile and fermented glucose, lactose, maltose, and mannite, with the production of acid and gas, but caused no change in saccharose or dulcite; rendered milk acid without producing any clot.

In all five of these cases there was intense inflammation of the intestinal mucosa practically throughout; in some, scattered petechiæ were present, but in no instance was there any ulceration. The contents were of a mucoid or mucopurulent nature, and in the Wild Cats in part hæmorrhagic. The mesenteric glands were swollen and some were pink from congestion.

Again, in my report for 1926, I referred to certain cases among the reptiles dying with a severe membranous form of the disease. The symptoms during life were obstinate diarrhœa, the evacuations being, in very acute cases, blood-tinged and at times containing portions of slough. The morbid changes seen at autopsy were an acute inflammation of the bowel usually more intense towards the lower part, and a mucosa covered or replaced by an ashy-grey membrane, the wall of the bowel being not only inflamed, but thickened and œdematous. Secondary abscesses were not infrequently present in the liver from the development of a portal pyæmia. The organism obtained from the portal blood, the liver, the splenic pulp, and the depths of the intestinal mucosa in those which were sufficiently fresh to offer any hope of successful bacterial cultivation, was a Gram-negative bacillus, actively motile, producing acid and gas in dextrose, maltose, and mannite, acidifying but not clotting milk, producing indol in four or five days in peptone media, but having no action on lactose or dulcite.

Thirdly, three Hamadryas Baboons died early in the year, showing the same pathological changes as those described in a small outbreak among these Baboons in 1925—namely, an acute inflammation of the small intestine with ulceration in the lowest part towards the ileo-cæcal valve From two of these was isolated a bacterium giving the reactions of *B. ærtrycke*, type "Mutton." This had been found in 1925 and confirmed by Prof. Ledingham, of the Lister Institute; and as since then I had obtained some potent immune serum for this bacillus, I was able to prove it serologically as well as culturally and morphologically in the present instance. Dr. Vevers was at once informed of this result, and measures were taken by him which proved eminently satisfactory, no further cases having occurred, and what might very easily have proved a devastating epidemic was averted.

Two cases have been included under the heading of "Enteritis" —namely, the Orang-utans, "Ginger" and "Nellie," Nos. 792 and 926/27, respectively. They were not instances of enteritis in the strict sense, death being due in each case to a severe Colitis of a dysenteric character, while the small intestine appeared healthy. In the former the inflammation started at the hepatic flexure, where the mucosa presented scattered petechiæ; these increased lower down, so that the descending colon and rectum showed an intensely inflamed surface with small crateriform ulcers, the intervening tissue being swollen only—in fact, a picture suggestive of amœbic dysentery in Man, though no Amœbæ were found in the tissues of this animal.

In the latter there was a different picture, though the area involved was the same. The mucous surface of the whole of the large intestine was acutely inflamed; in fact, the actual mucosa was practically removed, its place being taken by shallow, greenish-grey ulcers with sloughs, an almost gangrenous surface, with the small remnants of the mucous membrane red and angrylooking. In this case the condition more closely resembled that of human bacillary dysentery.

There is no need to dilate further on these. Mr. Reginald Lovell, who in September last was appointed to the staff of the London School of Hygiene and Tropical Medicine as Assistant to the Research Fellow in Comparative Pathology, has undertaken bacteriological investigations on some of the cases of enteritis and of pulmonary diseases here since he took over the duties of his appointment on October 1st, 1927, and appended to this report is a record of his investigations during the final quarter of the year.

5. *Rickets* and allied affections of the bones, including osteoporosis, osteomalacia, and osteitis fibrosa, have been more numerous among the mammals during the year, but avian cases have been less, so that (*vide* Table III.) the total is only three above that for 1926. Some of these had been but a short time in the Gardens, and had come in with the disease already established. Thus, a Red Tiger-Cat, *Felis aurata*, No. 419/27, died twelve days after arrival. The thorax was much deformed, the sternum being bent in about the middle so that the antero-posterior diameter of the thorax was narrowed to half. The ribs were soft and showed much beading, and the wrists were swollen at the epiphyses. An important condition, perhaps the actual cause of death, was a severe diaphragmatic hernia, the whole stomach and part of the spleen having passed into the thorax by the pleuro-peritoneal opening.

Four others were Common Marmosets. These animals are often kept as pets by private individuals, are overfed, usually wrongly fed by their indulgent possessors, and when they become rachitic and ill, "having received every attention" and cossetting at home, they are deposited in the Society's Gardens, in some cases *in extremis*. Some die from the rickets, the fatal issue being accelerated by a broncho-pneumonia or by fretting. Two such died in August, one after 9 days, the other in 12 days.

Two other Marmosets, Nos. 756 and 812/27, which had been here 3 and 4½ months respectively, showed an extreme grade of the osteomalacic or soft-boned type of the disease. The sternum in each case was deformed and much bent, the ribs could be folded up without breaking, the limb-bones could be curved for more than a quarter of a circle without fracture, the bones of the pelvis were unduly soft, and those of the calvarium were indentable with slight pressure.

In a Lion-Marmoset, *Leontocebus rosalia*, No. 696/27, there was a mingling of the two conditions. The various lesions need not be described in detail, but the chief were a deformity of the sternum, which was bent at a re-entrant angle of 90 degrees; the ribs were markedly compressed laterally, distorted and beaded, both internally and externally. The epiphyses of the long bones were not enlarged, but the bones themselves were softer than normal, and slight pressure resulted in the production of green-stick fractures.

Two others, a Gambian Mongoose, *Arielu gambianus*, No. 467/27, and an African Civet-Cat, *Civettictis civetta*, No. 669/27, showed signs of the disease on arrival, and it was hoped that careful feeding, skilled attention, and good hygiene would eradicate the malady. The condition, however, was too advanced, and the persistent absence of sunshine during the summer months has probably played no small part in keeping up the numbers of cases of rachitic affections.

A Patas Cercopitheque, No. 778/27, which has been in the Gardens for 16 months, showed signs of rickets which must have been at one time very severe, but which had apparently greatly improved. Death was the result of broncho-pneumonia, and some at least of the deformities were due to old fractures which had healed. Both femora were bent and much thickened about the middle, and had possibly been the sites of fractures; the left radius and ulna had been broken at the junction of the upper three-fifths with the lower two-fifths, and had united with much irregular callus; the right forearm had also been broken about the middle, and had healed with rather less callus-formation. Both humeri were bent, and the shafts were thickened and buttressed, but showed no fractures.

Incidentally, the fact may be mentioned that another Patas Cercopitheque died on the preceding day from broncho-pneumonia also with rickets, and presented an ununited, though not very recent, fracture of its left femur.

In this connection the case of a Nubian Giraffe, No. 116/27, is of interest. This had been 7 months in the Gardens. For the last three days of its life it had given evidence of weakness in the hind limbs, and just before death was attacked with spasmodic convulsive movements of the limbs. On opening the vertebral canal, the meninges were seen to be blue in colour and bulging, owing to hæmorrhage into the membranes and within the cord itself. This was extensive and involved the whole lumbar and the lowest third of the thoracic cord, less marked in the middle third and fading away above this. There was, further, a subarachnoid hæmorrhage over the left cerebral hemisphere. The case is mentioned here because, in addition to the hæmatorachis and hæmatomyelia, the vertebræ were very soft and could almost be cut with a knife. Whether there was any general vascular defect, it is impossible to state, but the fact may be noted that there was a large hæmangioma in the right lobe of the liver, occupying an area the size of a cricket-ball. It is possible, though purely a matter of conjecture, that there was an analogous condition of a varicosity of the spinal veins, which had given way, but none such was found at autopsy, the hæmorrhage being an extensive one.

Lastly, the case of "Oojah," the Pigmy African Elephant, *Loxodon pumilio*, No. 631/27. This animal was believed to be between 7 and 8 years of age at the time of death, having been here 2 years 4 months. Soon after arrival she began to show signs of lameness and swelling of the legs. The use of ultra-violet rays and other forms of treatment from time to time appeared to benefit, but only temporarily. Special boots were made for her, but they needed frequent alteration, and later caused chafing and seemed to be a source of much discomfort. X-ray examination showed not only no improvement, but an apparently spontaneous fracture of the left radius occurred. She became very miserable and for the last three weeks was barely able to stand, and euthanasia was decreed and carried out by means of intravenous injection of morphine. The conditions found at autopsy were of much pathological interest. A brief statement of the bony changes may be mentioned first. The fore-limbs were swollen at the wrist-joints and considerably deformed; the left radius was fractured near the lower epiphysis—in fact, so near that there was some doubt as to whether the lesion was not in part a separation of epiphysis; there was a good deal of poorly-ossified callus. The left hind limb was swollen and the bones soft and becoming twisted and deformed. All the bones were unduly soft; the sternum could be cut through with a knife, and in the upper part the interior was seen to be diffusely cancellous surrounded by thick cartilaginous tissue; lower down, at the level of the fourth rib, it became almost entirely cartilaginous with faint attempts at bone-formation in the interior. The skull-bones were very soft and could be sliced away with an ordinary knife down to the meninges; there was no separation of the bones into tables, no diploë, but a uniform suety consistence throughout. The vertebræ also could be cut through without difficulty.

As regards changes other than those of the bones, the only abnormalities found were four ulcers of a chronic character, with smooth, rounded margins, at the pyloric end of the stomach, and in the common bile-duct were long nematodes (*Gramocephalus clathratus*), many of them with their heads buried in the ulcers of the mucosa. No abnormality was found in the heart or lungs. The heart itself weighed 2150 gm.; the aorta measured 21 mm. in internal diameter and the wall itself was 5 mm. in thickness. The thyroid was pale, but was not obviously abnormal.

The pituitary appeared to be small, but the normal size of this I am unable to state. Apart from the size, however, it seemed to be shrunken, fibrous, and a little shrivelled, and is to be the subject of special investigation. It may be that this condition of the pituitary has some connection with the "pigmy" character, and that these are not a distinct genus of elephant. This, however, is mere conjecture, and only further autopsies can decide.

Portions of the skull and of the long bones were sent to Mr. Lawford Knaggs, F.R.C.S., and he reports that the condition is a good example of *Osteitis fibrosa*.

Of the six Avian cases, 5 were in-bred Budgerigars and call for no detailed account. The other was a Cockatiel, *Calopsittacus novæ-hollandiæ*, No. 754/27, which had sustained a severe fracture of the left tibia. This had healed badly, with marked inversion of the foot. The bones of the thorax, ribs, and sternum were very soft; the calvarium was thin and could be easily indented, and when removed could be rolled up without fracture; the vertebræ were soft.

The only Reptilian case was a Tuberculated Iguana, No. 296/27, whose limb-bones were swollen, soft, and distorted, and those of the skull thin and indented with slight pressure. There is nothing particular to note about this.

6. *Pulmonary Conditions*, apart from Tuberculosis and Mycosis.

Instances in which capillary bronchitis or broncho-pneumonia was diagnosed as the cause of death have been considerably less in number than in 1926—in fact, a reduction of more than a third. In the previous year's report these cases were not separated from those of lobar pneumonia, and if both are added together for purposes of comparison, the total deaths from these pulmonary affections show a satisfactory decrease.

In the last three years there have been 153, 95, and 72 respectively. The following Table gives the distribution of these among the different Orders.

TABLE IV.

	1925.	1926.	1927.
Mammalia	43	22	17
Aves	84	37	32
Reptilia ..	26	36	23
Total	153	95	72

DEATHS FROM LOBAR PNEUMONIA AND CAPILLARY BRONCHITIS FROM 1925–1927.

For purposes of comparison, it will be safer to regard the figures for lobar pneumonia rather than the combined. Where examination fails to reveal any morbid condition other than the broncho-pneumonia (or capillary bronchitis), provided this is fairly extensive, the death is assigned to this cause; but it is only right to say that in many others there is a certain degree, and a very varying degree, of capillary bronchitis which may have taken a share in causing death or may be merely a terminal event. When other conditions sufficient to bring about a fatal issue have been found, death has been ascribed to the latter, and such are not included. This is not altogether satisfactory. To give but a single reason. An animal, more often a bird, is ill from a slight degree of catarrhal bronchitis or early broncho-pneumonia, perhaps associated with a similar condition of the intestine, and it is set upon by its companions and dies from cerebral hæmorrhage, the result of a penetrating wound of the skull; or, we need not accuse its companions of murder, but the bird feeling ill falls off its perch on to its head and sustains a fracture of the skull or intracranial hæmorrhage. There is no doubt that the primary cause of death was catarrhal inflammation of the lungs, at the same time quite inadequate of itself. In other words, the category of broncho-pneumonia is not a hard-and-fast one as in the case of lobar pneumonia, but leaves a good deal—too much for satisfactory scientific record—to the interpretation of the pathologist, the personal factor.

These cases will not, therefore, be spoken of in detail in this report, with one exception, the Chimpanzee, "Clarence," No. 944/27. He had been here for 1¾ years. Four days before his death he was taken ill with fever, not very high, 101–102° F., only and severe dyspnœa. The respiratory distress and rapidity of respirations increased until death. At the autopsy the lungs showed extensive broncho-pneumonia involving all lobes severely, and pus exuded from the bronchioles. The bronchial glands were swollen and congested. Bacteriological investigations were undertaken by Mr. Lovell, whose report appears on p. 101.

Of the cases of Lobar pneumonia the two following are of interest amongst the mammals. The first as an example of how severe disease can be without any signs indicative of illness, the second for the bacteriological findings and for the pathological analogy with the disease in Man.

The former was a Burmese Muntjac, *Muntiacus muntjak grandicornis*, No. 237/27, 5½ years old, having been born in the Gardens. It was seen running about, and to all appearances in its usual health and taking its food well on the day before its death. In addition to the pathological findings about to be described, this animal was pregnant with a calf very nearly at full term. At the autopsy there were seen to be old pleural adhesions over both lungs. On the visceral surface of the right pleura and over the diaphragmatic surface there was fibrino-purulent deposit. The lung was pneumonic, solid, and sank in water as a whole. The left lung, except for a certain degree of hyperæmia, was not affected. The pericardium was covered with a layer of fibrino-purulent deposit, and the pericardial cavity contained fully 500 c.c. of blood-tinged purulent fluid, the pericardium being also coated with a yellow purulent deposit containing fibrin.

The second was a Grey's Monkey, *Cercopithecus greyi*, No. 816/27, which arrived in the Gardens eight days prior to its death. At the autopsy the right lung was found to be entirely solid, in a state of grey hepatization, while the upper lobe of the left was also solid, but in the condition of red hepatization; the lower lobe of this lung was not involved. With the exception of an infection of the bowel with cestodes and nematodes, the other organs were normal. Sections of the tissues when stained showed the typical changes of the two stages of red and grey hepatization as seen in human cases, and cultures were made from the tissues as described in Mr. Lovell's report.

The only avian case worthy of special mention is the All-green Parrakeet, No. 941/27, already referred to under the section on Tuberculosis. As stated, there was alimentary tuberculosis with infection also of the liver and spleen and slight also of the lungs, but death was due to a double lobar pneumonia.

The following is Mr. Reginald Lovell's report of his investigations into the bacterial aspect of some of the cases of enteritis and respiratory disease during the last quarter of 1927:—

The following is a brief description of some of the cases of interest which have been dealt with bacteriologically during the last quarter. One must, of course, realize that bacteriological research is of necessity a slow process, and the results of only a few cases are yet available. There are many difficulties to be overcome in such work, one of the greatest arising when we have to deal with an animal which has been dead more than two or three hours before coming to autopsy. Putrefactive organisms from the intestine very soon invade the tissues, and even if the causal organism is still present, the difficulty of isolation is increased. This is especially so when dealing with reptiles, as the risk of contamination with putrefactive bacteria is enhanced owing to the carcase having remained in the warmer atmosphere of the Reptile House. It will thus be seen that all animals which appear to have died from some bacterial invasion are not necessarily suitable for bacteriological examination.

One further point may be noted. In the following communication it will be observed that several types of bacteria are described, but no name is given. It is not always possible to classify them, because many appear to be different from any of the well-known species which attack Man or the domesticated animals, and there is little literature on the bacteria which invade wild animals, whether in their natural habitat or in captivity, to which one can refer. It has been possible, however, in several instances to classify them to some extent and to indicate their pathogenic rôle in respect to Man.

RESPIRATORY DISEASES.

Two of the respiratory cases which have been investigated are of interest, as they serve to distinguish between two of the main types of pneumonia.

A Gray's Monkey (*Cercopithecus grayi*), No. 816/27, came to autopsy on the 29th of Oct., 1927. The right lung was solid and in a state of grey hepatization, and the upper lobe of the left lung showed red hepatization. The technique employed in the isolation and identification of the causal organism was a modification of that employed by Avery and his co-workers of the Rockefeller Institute in their researches on lobar pneumonia in human beings. An organism giving the following characteristics was isolated, viz.: a Gram-positive capsulated diplococcus, lethal to a mouse, and giving typical flat-ringed colonies with *α* hæmolysis on blood-agar medium. The bile solubility was tested by treating 30 drops of a suspension of the diplococcus with 3 drops of a 10-per-cent. solution of desoxycholeic acid which had been rendered alkaline to phenolphthalein. The suspension appeared quite clear in five minutes. Agglutination experiments were put up against previously-prepared anti-pneumococcal sera of the Rockefeller types I., II., and III., and no agglutination took place. This was repeated with a similar result. There can be no doubt that the cause of death in this animal was acute lobar pneumonia due to infection with a pneumococcus Group IV.

A Chimpanzee, "Clarence" (*Anthropopithecus troglodytes*), No. 944/27, was ill for a few days before death with a severe dyspnœa and symptoms of broncho-pneumonia. At autopsy both lungs showed excessive broncho-pneumonia and there were weak pleuritic adhesions. A similar technique was employed, but whereas the injected mouse died in 18 to 24 hours in the previous case, this experimental mouse did not die for 10 days. It is presumed that the mouse was recovering from infection with an avirulent pneumococcus, because there were many pneumococci present in the peritoneal exudate, but they failed to grow on blood-agar, or in blood-broth, and were probably dead, and the sudden cold weather at this period was, it is believed, the actual cause of its death. The organism however proved to be a Gram-positive capsulated diplococcus, and the suspension of dead cocci washed from the peritoneum of the mouse was soluble in bile (10 per cent. desoxycholeic acid), and was not agglutinated by the pneumococcal sera Types I., II., or III. One can at least say that an avirulent Group IV. pneumococcus was present although not isolated.

Direct culture revealed no pneumococci but Gram-negative bacteria, which failed to grow on plain agar but which grew well on Fildes's agar and in Fildes's broth. Cultures produced neither indol nor hæmolysis. These findings, taken in conjunction with the microscopical characters, point to the organism as Pfeiffer's influenza bacillus.

It is obvious that both the pneumococcus and Pfeiffer's influenza bacillus were present in the depth of the lung, but one hesitates to state definitely that "Clarence" died from influenza, although the evidence is strong. Whatever is the cause of influenza in Man, it may not be out of place to mention that the combination of these two organisms has been found in many cases of influenza in recent epidemics, and Pfeiffer's bacillus was at one time held to be the actual cause of the condition. Recent research indicates that both are at least associated with influenza.

ENTERITIS.

Many cases of enteritis have been investigated amongst birds, mammals, and reptiles, and will be treated under those headings.

Aves.

(1) A Green-billed Toucan (*Rhamphastos dicolorus*), No. 743/27, was subjected to autopsy on 4. 10. 27, and cultures were taken from the bile, portal blood, intestinal contents, and systemic blood. From the intestinal contents and systemic blood was isolated a Gram-negative coliform bacterium giving acid and gas in dextrose and no reaction in mannite, maltose, lactose, sucrose, and salicin. Gelatine was not liquefied, indol was produced, and litmus milk rendered alkaline. Intra-peritoneal injection into a mouse of 0·5 cm. of a 24-hour broth culture proved lethal, and a similar organism was recovered from the blood of the experimental animal in both cases. Definite motility even after one or two subcultures was not established, but otherwise this organism appears to be identical with *Bact. morgani*, and reference to its significance will be made later in this communication. Two other types of coliform organisms were isolated from the bile and portal blood respectively. They do not conform to any well-known species either in human or veterinary bacteriology. The one from the portal blood proved to be pathogenic to a mouse. As a double infection is not uncommon in such conditions, its pathogenic rôle is probable. It produced acid and gas in dextrose, maltose, and mannite, and after 14 days gave acid and gas in salicin and acid in lactose Gelatine was not liquefied, indol was produced, and litmus milk rendered alkaline.

(2) A Bateleur Eagle (*Helotarsus ecaudatus*), No. 988/27, died from acute enteritis on 21. 12. 27. Cultures were taken from the blood, liver, spleen, and the intestinal wall. A peculiar organism was isolated from the latter—viz., a Gram-negative coliform bacterium which gave acid and gas in dextrose and maltose, and no reaction in mannite, lactose, sucrose, and salicin. Gelatine was not liquefied, litmus milk was rendered alkaline, indol produced, and the organism was non-motile. It proved to be pathogenic to a mouse, and a similar organism was recovered from the blood of the experimental animal. From the blood of the eagle was isolated *Bact. fæcalis alkaligenes*, which is not usually regarded as pathogenic in Man, although it has been isolated several times during the previous year by Dr. H. H. Scott from reptiles and a Levaillant's Amazon *.

(3) A Bonelli's Eagle (*Eutomactus fasciatus*), No. 995/27, proved of interest from a bacteriological point of view. At autopsy acute inflammation of the intestine was revealed with a false membrane over portions of the duodenum and jejunum.

---

* "Report on the Deaths occurring in the Society's Gardens during the year 1926," P. Z. S. April 6th, 1927, pp. 185–186.

Cultures from the blood and liver proved sterile, but an unknown organism was isolated from the spleen and intestinal mucosa. This proved to be a small Gram-negative bacterium growing singly and in long chains. It stained unevenly and was motile. Growth on McConkey's medium was good, and the following fermentation reactions took place: acid but no gas in dextrose and maltose, and on the fourth day acid in salicin, and on the fifth acid in lactose. Gelatine was not liquefied, litmus milk was rendered faintly acid, and indol was produced. Cultures of this organism and also the one from the previous case are being kept, and further investigation will be carried out at a later date.

Mammalia.

This group of cases is very interesting, as *Bact. morgani* has been isolated from a number of them and there is some evidence of infection in sequence.

(1) An Orang-utan, "Ginger" (*Simia satyra*), No. 792/27, was removed from the North Mammal House to the Sanatorium. Death occurred on 21. 10. 27, and was found to be due to a severe colitis. The detailed changes have already been given in Dr. Scott's report. Cultures were attempted from the spleen, portal blood, systemic blood, and intestine, and *Bact. morgani* was isolated from the latter site.

(2) An Orang-utan, "Nellie," No. 926/27, was also removed from the North Mammal House to the Sanatorium when "Ginger" became ill, but she died on the 6. 11. 27. Cultures were made from the spleen, kidney, bile, mesenteric glands, blood, intestinal mucosa, and intestinal contents. Only from the latter was *Bact. morgani* isolated. From the intestinal mucosa another organism was isolated, namely one that gave similar sugar reactions to *Bact. morgani* and was lethal to a mouse, but it liquefied gelatine, did not produce indol, and after five days partially-digested litmus milk. It is possible that this should be classified as a *Bact. proteus*, but it is mentioned because of its appearance in another case and its affinity to *Bact. morgani.*

(3) A Squirrel-Monkey (*Saimiris sciurea*), No. 952/27, died in the Sanatorium from enteritis on 15. 12. 27. The intestines were congested and the mesenteric glands swollen. Cultures from the liver, bile, spleen, blood, and intestinal mucosa gave no information. *Bact. morgani* was, however, isolated from the intestinal contents.

(4) A Naked-ear Squirrel-Monkey (*Samiris usta*), No. 972/27, also died in the Sanatorium on 19. 12. 27. A condition of enteritis was found at autopsy, and Filariæ was present in the peritoneum and mesentery. The intestine was pink and congested and the mesenteric glands swollen, but the condition appeared to be less severe than in the former case. Cultures from the liver and mucosa gave no pathogenic organisms, but

from the intestinal contents was isolated an organism identical with the gelatine-liquefying one grown from the intestinal mucosa of the second Orang-utan, "Nellie."

Reference may be made at this point to the observations of workers on Summer Diarrhœa in children. Although the bacteriological findings are varied, yet the organism that has been found most frequently is *Bact. morgani*, and Morgan and Ledingham regard it at least as an important factor in the cause of the disease. Other workers affirm that there is in Summer Diarrhœa a general increase in the number of non-lactose-fermenting organisms in the fæces, chiefly consisting of *Bact. dysenteriæ*, *Bact. morgani*, and *Bact. proteus*. Another point of note is the evidence which has been brought to show that *Bact. morgani* is relatively unable to penetrate the intestinal mucosa, and this probably accounts for its non-cultivation from any of the body-tissues. Only in one case, namely the Green-billed Toucan, was the organism in question isolated from anywhere but the intestine.

A further case of interest in the Mammalia is:—

(5) A Mona Cercopitheque (*Cercopithecus mona*), No. 906/27, which at death revealed mycosis of the liver and spleen and a gastro-enteritis. Cultures from a Peyer's patch gave a *Bact. proteus* and various lactose-fermenting organisms. From the bile and liver was isolated an organism which was at first thought to be a dysentery bacterium of the Flexner type. It was a non-motile cocco-bacillus with occasional filamentous forms and produced acid in dextrose, maltose, and mannite, with no reaction on lactose and sucrose. At a later stage (fifth day) it did, however, ferment salicin which *Bact. dysenteriæ* (Flexner) does not. Gelatine was not liquefied, nor was indol produced; litmus milk was rendered alkaline. The organism proved to be pathogenic to a mouse, and a similar bacterium was recovered from the experimental animal. No name is given to this organism as it does not exactly correspond with any of the known bacteria, but it is closely allied to the dysentery group, and, as in other cases, stock cultures are kept for further investigation.

Reptilia.

Several cases among reptilia in which the intestine was inflamed have been investigated, but, as already stated, it is a matter of great difficulty to determine the ætiological significance of organisms isolated when once putrefactive contamination has entered. In most cases *Bact. proteus* has been present. Two cases are worthy of note and are mentioned, although investigation into the organisms is not yet complete.

(1) An Anconda (*Eunectes murinus*). No. 847/27, died on 7.11.27 from a membranous enteritis followed by perforation and consequent peritonitis. It had been passing sloughs for some time previously and the bowel was inflamed and gangrenous. Other lesions were present in the liver and kidneys.

From the blood was isolated a non-motile coliform organism giving the unusual reactions of producing acid only in dextrose, but acid and gas in maltose, and causing no change in mannite, lactose, sucrose, and salicin. Litmus milk was rendered alkaline and gelatine was not liquefied. Further cultures were incubated and the same result occurred. It was pathogenic to a mouse by intra-peritoneal inoculation and was recovered from its blood. *Bact. proteus* was also isolated from the pericardium and liver.

(2) A Reticulated Python (*Python reticulatus*). No. 932/27, also died from a membranous enteritis on 8.12.27. Cultures from the blood were sterile, but from the bile and intestinal wall the following organisms were isolated: a motile coliform bacterium which seems to belong to the *Bact. paratyphosus* B group. A similar result was obtained from the liver, but this strain fermented salicin with the production of gas after 14 days. The other two strains after incubation for 28 days have not produced acid in salicin, sucrose, or lactose. Agglutination experiments have been attempted against specific and non-specific sera of this group, but no reaction took place. Further serological work is being undertaken, as it is of the utmost importance to establish whether this is a known or new species of the group.

PYÆMIA.

A case of exceptional interest is that of a Viscacha (*Lagostomus trichodactylus*), No. 826/27, which died on 2.11.27. In addition to a thickening of the mitral valve the kidney showed many abscesses. On examination of films from the kidney abscesses Gram-positive cocci in tetrads and short chains were seen. A pure culture of *Micrococcus tetragenus* was grown which on intra-peritoneal inoculation killed a mouse in 24 hours, and when inoculated subcutaneously a sub-culture killed a mouse in 16 days. In each case the micrococcus was recovered. The biochemical reactions were: acid in dextrose, mannite, maltose, lactose, and sucrose, but no reaction in salicin. Gelatine was not liquefied and litmus milk was rendered acid, this being followed by partial digestion at a later stage.

Cases of septicæmia due to this coccus appear to be rare in Man in this country, although quite a number have been recorded on the Continent.

R. LOVELL, M.R.C.V.S., D.V.S.M.

The following is a list of Protozoal parasites found in examinations of blood-smears. These are made from all animals submitted to autopsy and sent to Dr. C. M. Wenyon, F.R.S., who presents for the information of the Prosectorial Committee a report of his findings each quarter. Smears are also made by us at the same time, and any found positive are kept for future reference. The list below is compiled by combining the several reports from Dr. Wenyon.

SINGLE INFECTIONS.

PARASITES.	HOSTS.
Hæmogregarines (107)	*Acanthophis antarcticus*; *Ancistrodon piscivorus* (6); *Bitis arietans* (2); *Boa constrictor* (3); *Calotes mystaceus* (3); *Chlorophis neglectus* (3); *Cinixys belliana*; *Cœlopeltis monspessulana* (3); *Coluber catenifer*; *Coluber corais* (2); *Coluber obsoletus* (2); *Coluber quatuorlineatus*; *Coluber vulpinus*; *Coronella getula* (3); *Coronella getula* var. *boylii*; *Coronella triangulum* (2); *Crotalus atrox*; *Crotalus confluentus* (4); *Crotalus exsul* (4); *Crotalus horridus* (2); *Crotalus scutellatus* (2); *Cyclagras gigas* (2); *Dendraspis viridis*; *Dipsadomorphus dendrophilus*; *Dryophis mycterizans*; *Elaphe oxycephalus*; *Elaps guttatus*; *Eunectes murinus* (3); *Heterodon platyrhinos*(2); *Iguana tuberculata*; *Lacerta ocellata* (3); *Laticauda colubrina* (5); *Lichamera roseopisca*; *Naja bungarus* (2); *Naja hajæ*; *Naja hannah*; *Naja tripudians*; *Natrix taxispilotus*; *Passerita mycterizans*; *Philothamnus semivariegatus*; *Psammophis sibilans*; *Psammophis subtæniatus*; *Python molurus*; *Python reticulatus* (2); *Python sebæ* (2); *Python spilotes*, *Rana pipiens*; *Rana tigrina*; *Sistrurus miliarius*; *Testudo ibera*; *Trionyx gangeticus*; *Tropidonotus fasciatus* (2); *Varanus bengalensis* (3); *Varanus exanthematicus* (2); *Varanus griseus*; *Varanus niloticus* (2); *Zamenis dahlii* (2); *Zamenis flagelliformis*; *Zamenis mucosus* (4).
Hæmoproteus (27)	*Alectoris græca vera*; *Balearica pavonina* (2); *Cerchneis tinnunculus*; *Circus macrurus*, *Coracias abyssinicus*; *Dasyptilus pesqueti*; *Eremapteryx leucotis*; *Eulabes religiosa*; *Grus antigone*; *Loriculus galgulus*; *Mimocichla rubripes*; *Munia oryzivora*; *Necrosyrtes monachus*; *Numida mitrata*; *Nycteria americana*; *Otogyps calvus*; *Pseudogyps africanus*; *See-see* Partridge; *Serinus* (2); *Serinus flaviventris*; *Serinus icterus*; *Sporæginthus melpodes*; *Steganurus paradisea verrauxi*; *Textor niger*; *Uræginthus phenicotis*.
Hæmocystidium	*Naja nigricollis*.
Plasmodium præcox (3)	*Cygnus melanocoryphus*; *Francolinus bicalcaratus*; *Rollulus roulroul*.
Lankesterella (3)	*Rana palustris*; *Rana tigrina* (2).
Leucocytozoon (4)	*Ptilogenys cinereus*; *Serinus canarius* (2); *Spinus citrinellus corsicanus*.
Hexamita	*Calotes mystaceus*.
Trichomonas (2)	*Testudo ibera*; *Tropidonotus ordinatus*.
Filarial embryos (7)	*Agapornis cana*; *Cittocinchla macrura*; *Garrulax leucolophus*; *Munia atricapilla*; *Paroaria cucullata*; *Paroaria larvata*; *Struthio australis*.

Double Infections.

Hæmoproteus and Plasmodium præcox (2).	*Argusianus argas*; *Leptoptilus crumeniferus.*
Hæmoproteus and Filarial embryos.	*Numida coronata.*
Filarial embryos (two types)	*Canis adustus.*
Hæmogregarines and Filarial embryos.	*Coluber melanoleucus* (2).
Hæmogregarines and Lankesterella (3).	*Rana tigrina* (3).
Lankesterella and Trypanosomes.	*Rana tigrina.*
Trypanosomes and Filarial embryos	*Ælurœdes viridis.*

Triple Infections.

Hæmoproteus, Plasmodium præcox, and Filarial embryos.	*Pyrrhuloxia sinuata.*
Hæmoproteus, Leucocytozoon, and Trypanosoma.	*Ptilogenys cinereus.*
Hæmoproteus, Leucocytozoon, and Filarial embryos.	*Athene noctua bactriana.*

The foregoing pages have consisted of remarks upon the various subjects mentioned in Table III. A report of the year's work would, however, be very incomplete if no reference were made to the many other matters of pathological interest which have been encountered in the course of routine autopsies. These questions will now be briefly dealt with. Some are of sufficient importance to call for a few details, while some will, it is hoped, be made the subject of special papers in the future.

1. Among the foremost of these are cases of CARDIAC AND CARDIO-VASCULAR DISEASE, of which there seems to have been an unusually high proportion. The following is a list of these :—

(1) *Congenital Defects of the Heart.*

(*a*) Thar, *Hemitragus jemlaicus*, No. 641/27. At the base of the septal cusp of the aorta, in the membranous part of the interventricular septum, was an opening 1 cm. in diameter with hard, calcareous edge, admitting of free intercommunication between the ventricles. There was intense atheroma of both the systemic and pulmonary aortæ, and the aortic semilunar valves were calcareous. This animal has been 11 years 5 months in the Gardens, and has already been mentioned under the heading of Tuberculosis, as this disease was also present.

(*b*) A male De Brun's Wallaby, one of Mr. Frost's collection, not taken on the strength of the Menagerie but housed in the Sanatorium. This animal had a large well-marked patent *Foramen ovale* in the interauricular septum.

(2) *Valvular Disease of the Heart.*

There are three examples of this among mammals and one avian case:—

(*a*) Mozambique Cercopitheque, *Cercopithecus rufoviridis*, No. 46/27, 5 years 10 months in the Gardens. This was an old warrior who had lost an eye in some bygone fight. A well-marked vegetation was present on the mitral valve and there was considerable myocarditis, the wall of the ventricle being thinned in places and tough.

(*b*) Hairy Armadillo, *Euphractus villosus*, No. 805/27, with vegetations on the flaps of the mitral valve. Death was due to abscess of lung with double empyema. In both pleural cavities was thin, brick-red purulent fluid, with flakes of lymph; the right contained much the larger quantity, 180 c.c. being measured and some 20 c.c. remaining. In the right lung, subapical in position, was an abscess measuring 1·5 cm. in diameter over which the pleura was weakly adherent and gangrenous. The lung was much compressed by the accumulated pleuritic effusion.

(*c*) Viscacha, *Lagostomus trichodactylus*, No. 826/27. 2¼ years in the Gardens. In this animal there was marked thickening and sclerosis of the mitral valve-flaps, with firmly attached ante-mortem clot. Death was due to a condition of pyæmia. In the liver, which was paler than normal, soft and very friable, were sparse miliary abscesses. In both kidneys were many small abscesses mainly in the cortex, but a few also in the medullary portion, varying in size from mere points to 3 mm. in diameter. The organism isolated from this and seen in smears and sections of the tissue was *Micrococcus tetragenus*.

(*d*) The avian case was a Violet-necked Cassowary, *Casuarius violicollis*, No. 318/27. The right auricular appendage was occupied by a large fungating vegetation with a broad base, adherent to the endocardium and ulcerated at the upper part of the periphery of this base. In the left side of the heart the mitral valve-flaps were thickened, hard, and contracted, with a "button-hole" opening 7 mm. in diameter, like the so-called Corrigan valve of human pathology. The myocardium of the left ventricle was hard, tough, and fibrous.

(3) *Aneurysms.*

(*a*) A Common Rat, blue variety, *Rattus rattus*, No. 324/37, with an *aneurysm of the heart*. In the right ventricle, between the columnæ carneæ, was an aneurysm 5 mm. in diameter containing some laminated clot. Both ventricles showed small pale areas of myocardial degeneration In this animal there are also, in the duodenum 2 inches beyond the pylorus, a small aperature leading into a diverticulum the size of a haricot bean, occupied by a fæcal concretion.

(*b*) Scarlet Tanager, *Rhamphocœlus brasilius*, No. 824/27, nearly 4½ years in the Gardens. When the body was opened an extensive blood-clot was seen covering the heart posteriorly and the lungs anteriorly. There was mycotic infection of the left anterior air-sac. The blood-extravasation had come from a ruptured *aneurysm of the left aorta*. Between 1 and 1·5 cm. above the base of the heart was a globular aneurysmal dilatation presenting a small perforation on its posterior aspect. Being above the level of the reflection of the pericardium, there was no hæmorrhage in this cavity, as in a former specimen (now in the Museum of Comparative Pathology of the London School of Hygiene and Tropical Medicine).

(4) *Rupture of the Heart.*

An American Tree-Sparrow, ***Spizella monticola***, No. 56/27, when apparently in perfect health suddenly fell dead. An extensive hæmorrhage was found filling the retrocardiac space between this organ and the liver, spreading over the anterior surface of the liver, and tracking down the left side and largely filling the pelvic. The blood came from a rent in the posterior surface of the right auricle. The proximal cause of this could not be discovered. There was no indication of aneurysm nor of any parasitic infection, and there was no bruising of the sternum or pectoral muscles.

(5) *Hæmopericardium.*

A Ring-necked Parrakeet, ***Palæornis torquata***, No. 800/27, showed at autopsy a pericardium distended with blood, partly clotted. There was no atheroma of the large vessels, but the left ventricle was much hypertrophied; there was hæmorrhagic extravasation also in the myocardium, and the kidneys showed a severe grade of chronic interstitial nephritis.

Seeing that there was no signs of aneurysm or wound of the heart, perhaps it would be more correct to describe this case as one of hæmorrhagic pericarditis; on the other hand, there was no definite inflammation of the membrane seen and the bleeding may have come from ruptured capillaries associated with high pressure, itself a concomitant of chronic nephritis.

(6) *Pericarditis.*

There were five instances of this; in one the condition was of the adhesive type and in four it was purulent.

(*a*) A Yellow Baboon, ***Papio babouin***, No. 923/27, showed firm adhesions of old standing all over the left lung laterally and posteriorly, and in front to the pericardium. The layers of the pericardium were inseparably united, the pericardial cavity being totally obliterated.

(*b*) Coypu, ***Myocaster coypus***, No. 154/27, which had been born in the Gardens only three weeks before. Death was due to bronchitis and purulent pericarditis. The pericardium was thickened and opaque, and covered with a layer of pus and lymph. The myocardium was inflamed.

(*c*) Burmese Muntjac, No. 237/27, dying from lobar pneumonia and pericarditis with purulent effusion. This has been already spoken of in the section dealing with cases of Lobar pneumonia.

(*d*) Anaconda, ***Eunectes murinus***, No. 27/27. In the pericardial cavity, in flakes between firm adhesions of visceral to parietal layers, was inspissated pus. The membrane itself was very thick and tough, and towards the apex the ventricle was clothed with thickened, adherent pericardium containing cheesy pus.

(*e*) Water-pilot, ***Natrix taxispilotus***, No. 402/27. The layers of the pericardium were adherent generally, and between it and the heart itself was a thick layer of greenish-yellow pus. The lungs were œdematous and contained small purulent deposits, apparently in the bronchi, and at the lower pole of the left kidney was an abscess 1·2 cm. in diameter.

(7) *Severe Atheroma.*

(*a*) The Thar, No. 641/27, with extensive atheroma of systemic and pulmonary aortæ, has already been mentioned as it presented also a congenital cardiac defect.

(b) A Blue-fronted Parrot, *Amazona æstiva*, No. 700/27. This bird was said to be very old; it was believed more than 100 years. Death was due to a tear in the posterior aspect of the right lobe of the liver and consequent extensive hæmorrhage. Blood surrounded the heart and had passed down to the pelvis. When the blood was washed away the large vessels arising from the heart were prominent and stood out rigidly; they were markedly calcareous, typically "pipe-stem," and the thoracic and abdominal aortæ were similarly practically lined by deposition of calcium salts.

2. CASES OF INTESTINAL OBSTRUCTION.

There have been five instances of this, all amongst mammals.

(1) Prairie-Wolf, *Canis latrans*, No. 388/27. Two months old, born in the Gardens. There was an intussusception of the ileum 5–6 inches in length, 10 inches above the ileo-cæcal valve. There were several Ascarids in the stomach, duodenum, and small intestine and a condition of acute enteritis, with ulceration. Worms were present both above and below the intussusception; these, and an irregular peristalsis arising from the enteritis, may have started the intussusception.

(2) Prairie-Wolf, No. 421/27, with a large ileo-colic intussusception, fully 6 inches of the bowl protruding through the anus.

(3) Red Tiger-Cat, *Felis aurata*, No. 419/27, already referred to as a case of Rickets, with a diaphragmatic hernia through the pleuro-peritoneal opening.

(4) Thar, *Hemitragus jemlaicus*, No. 712/27, dying from a complication of injuries. The right lung had been penetrated by a fractured rib in the mid-axillary line, with the production of a large hæmothorax, the lung being compressed in a small space in the costo-vertebral recess. In the left iliac region was much bruising, the muscles of the abdominal wall had been torn, and through an opening 2 cm. in diameter has passed a knuckle of small intestine which was itself perforated and lay between the muscle and the subcutaneous tissues.

(5) Hairy-rumped Agouti, *Dasyprocta prymnolopha*, No. 857/27, with intussusception of the colon.

A sixth case may be mentioned, a Serval dying from acute enteritis, No. 208/27. When the body was opened a swelling was noticed in the pyloric half of the stomach; this proved to be due to the passage back through the pylorus of the succeeding 1½–2 inches of the duodenum. I can find no record of such an occurrence in human or animal pathology, and the specimen has been preserved.

3. INTESTINAL PERFORATION.

Nine instances have been met with during the year, of which four were mammals, three birds, one fish, and one reptile.

(1) *Mammalian Cases.*

(a) Green Cercopitheque, *Cercopithecus sabæus*, No. 86/27. Twenty-two inches below the pylorus was a perforation, 0·8 cm. in diameter, with a clean but shelving margin, partly sealed by a plug of lymph, but allowing fæcal matter to leak through. In the peritoneal cavity were 250 c.c. of thin purulent fluid. Perforation had occurred at the site of one of several ulcers.

(*b*) Bay Lynx, ***Felis rufa***, No. 666/27, in which the cause of death was peritonitis resulting from perforation of the duodenum by nematodes. 3800 c.c. of inflammatory fluid were measured from the peritoneal cavity. In this fluid were many round worms which had passed through the perforation, while one was seen in the act of emerging, the head and half the body being in the peritoneal cavity, the remainder still within the abdomen. The exudation was partly ascitic, for it was only coagulated in islands and there was marked polylobular cirrhosis of the liver, this organ weighing only 130 gm.

(*c*) Blackbuck, ***Antelope cervicapra***, No. 707/27, with a large hepatic abscess, as big as a water-melon. The reticulum had been perforated by a pin which had been swallowed and had been arrested in the meshes of the mucosa.

(*d*) Thar, No. 712/27, already mentioned; in this a knuckle of intestine had passed through a rent in the abdominal mural musculature, had become strangulated, and had perforated.

(2) *Avian Cases.*

(*a*) Little Blue Heron, ***Florida cærulea***, No. 123/27, dying from hæmorrhage the result of perforation of the stomach by a foreign body, a bristle. There was much blood in the stomach itself, and the bristle was partly within and partly outside the viscus, the peritoneum being inflamed over the site of the wound.

(*b*) West African Ostrich, ***Struthio camelus***, No. 303/27. Perforation of the gizzard by a foreign body—a tin-opener—which had caused death from hæmorrhage by further opening into the portal vein. In the abdominal cavity was a very large clot of blood. In another part of the gizzard, in a small diverticulum, was a pin which was nearly through the wall, and other foreign substances were present, namely a metal badge, a cent-piece, and two staples, one broken.

Another West African Ostrich, No. 346/27, which affords even a better example than the last of the proverbial digestion of an ostrich. Death in this case also occurred from hæmorrhage, owing to perforation of a vessel in the gizzard wall, though the viscus itself was not actually perforated. These two were the subject of a demonstration at a Scientific Meeting of the Society in June, but an enumeration of the contents, as a permanent record, will not be amiss. There were three handkerchiefs, three gloves, three feet of cord, two iron-wire staples complete and several fragments, a 4-inch nail, four halfpennies, two farthings, a franc, one motor-tyre valve, portion of a magneto-spanner, a collar-stud, a lead pencil, a picture-hanger, an alarum-clock winder, a watch-swivel, fragment of a locket-chain, a wooden film-roll, a screw, and sundry small pieces of metal.

(*c*) Denham's Bustard, ***Neotis denhami***, No. 1039/27. One inch below the pylorus was a perforation of the wall of the duodenum sealed by peritonitic lymph; no foreign body was found in connection with this. In the upper part of the left lobe of the liver, however, was a concretion the size of a walnut, 2·3×1·6×1·7 cm., surrounding a fragment of wire which had probably penetrated from the gizzard, although no sign of any perforation could be seen in that viscus. If it had occurred from the gizzard, it must have happened some considerable time previously for a concretion of such a size to have formed, and any wound which had resulted had completely healed.

(3) *Reptilian Case.*

This was an Anaconda, No. 847/27, which for several weeks prior to its death had been passing sloughs and membranous fragments with copious bleeding at intervals. The *post-mortem* findings were of interest. Over a length of 12–13 inches, ending about the same distance above the cloaca, the bowel was very inflamed, almost gangrenous. Near the lower limit of this area was a perforation measuring 4×3 cm. Above this there was a patchy membrane, but below a huge accumulation of membrane and débris heaped up to a thickness of 2 cm. Outside the intestine was a large collection of greenish pus extending from the stomach to the level of the cloaca, and fragments of food, pigeon-bones, feathers, etc., were seen passing from the intestine into this large abscess through the perforation. The liver presented numerous white foci—abscesses from a portal pyæmia—and the kidneys showed also small miliary abscesses; the pericardium was adherent, the cavity being obliterated and occupied by fibrinous and gelatinous coagulated lymph.

(4) *Piscine Case.*

A Wrasse died in the Aquarium and was sent up for examination. There was a ragged ulcer near the cloaca discharging pus in abundance and with protruding spicules of bone. One to one and a half inches above the cloaca was a ragged perforation of the intestine, 1 cm. in diameter, partly occupied by a slough and surrounded by a diffuse abscess. Half an inch below this perforation was a second, rather smaller, and several small perforations, each with protruding bones of whiting. There were seven separate perforations in all. The inflammation has been too acute for localization by peritonitic adhesions, and there was an extensive purulent peritonitis.

4. ACCIDENTS AND INJURIES.

(1) There have been 11 cases of *Rupture of the Liver*: six small birds, two Pheasants, a Teal, a Crossoptilon, and a Parrot.

In nine of these the right lobe was the one affected, in one the left, and in one both. The superior surface in one; the anterior aspect in two, in one of which the rent extended up slightly on to the superior surface; the right lateral surface in two, in one of these the tear extending forwards over the anterior surface; three times the inferior surface of the right lobe was the site of rent, in one of them extending some distance up the posterior surface, and in one (the Amazon Parrot, No. 700/27, already mentioned, with advanced atheroma), the posterior surface only. In only one instance, a Budgerigar, blue variety, No. 908/27, was the left lobe involved, on the inferior surface. Lastly, an Amherst's Pheasant, No. 1031/27, had sustained extensive injuries, among them two tears in the right lobe of the liver, one laterally and one anteriorly, and others in the left lobe. The pelvis was fractured and the right kidney was torn also.

(2) *Respiratory.*

(*a*) A Wild Cat, ***Felis sylvestris***, No. 34/27. Suffocated by regurgitation of food and passage of it into the larynx and trachea. Food was in the trachea and some impacted in the glottis; the lungs were frothy and the surfaces petechial.

(*b*) Female Hamadryas Baboon, No. 78/27, the widow of "Murphy," was wooed *en secondes noces* by four suitors simultaneously. A battle-royal ensued in which the lady suffered somewhat, and one of the gentlemen having gained a temporary advantage fled with her into the water, whither his rivals followed to renew the fight. When the final victor emerged, bringing with him his prospective bride, she was found to be dead, and, after holding a wake, he and his companions the next morning returned the body to the pond. At the inquest there were found many bruises and scratches, but not sufficient to cause death, which was definitely due to drowning. The case was duly recorded in the *Morning Post*.

(*c*) A Hog-nosed Snake, *Heterodon platyrhinos*, No. 672/27, died of suffocation from regurgitation of food, in the same way as the Wild Cat just mentioned.

(*d*) A Giant Cyclagras, No. 955/27, showed at death constriction round the neck, two inches behind the head, and the lung was intensely engorged, in fact hæmorrhagic, containing blood and mucus. It had been placed in a box, the lid of which was kept from falling back by means of a chain. A commotion was heard soon after the lid was closed, and was thought to be due to a fight between it and its companion, but when the box was opened, the snake was found to be dead, its head being encircled by the chain, which had strangled it.

(3) *Others of interest.*

(*a*) An African Civet-Cat, *Civettictis civetta*, No. 371/27, with a simultaneous and practically symmetrical transverse fracture of the humerus on each side. How this was produced is not known.

(*b*) Thar, No. 712/27, already mentioned. This animal had right-sided hæmothorax secondary to fracture of a rib and penetration of a lung, injury to the abdominal wall, rupture of muscle, protrusion of intestine, strangulation and perforation of the gut.

(*c*) Rusty-spotted Genet, *Genetta rubiginosa*, No. 928/27, which was chloroformed after it had inflicted serious injuries on itself. It had gnawed off all the toes of the hind foot and part of the tarsus and was bleeding very profusely.

There were a few instances in which injuries had been inflicted by companions which had either resulted in death or were so severe as to be beyond attempts at cure. These need not be mentioned in detail.

5. PYÆMIA.

Apart from cases of portal pyæmia, which are not very uncommon, particularly among Reptiles with severe infection, there have been five cases of general pyæmia. Two were mammals, two reptiles, and one bird.

(1) *Mammals.*

(*a*) Ibean Baboon, *Papio ibeanus*, No. 441/27, was unable to walk and died a fortnight after admission. Abscesses were found in the lungs, the spleen, the kidneys, in the bronchial, internal mammary, inguinal, and lumbar glands. The 3rd, 4th, and 5th dorsal vertebræ were exposed, caseous, necrotic, and exuding pus; below the right acetabulum was another abscess, but not communicating with the hip-joint, and there was an erosion of the right parietal bone of the skull. The spine appeared to be the oldest site. In view of the multiple abscesses in the lungs and kidneys, and the presence of indications of old infarcts in the latter, one might have expected to find an endocarditis, but none such was present.

(*b*) Viscacha, No. 826/27, with pyæmia and valvular disease of the heart, has already been mentioned when speaking of cardio-vascular conditions.

(2) *Birds.*

A Blue-bird, *Sialia sialis*, No. 383/27, with cellulitis of the feet, probably traumatic, from infection of fissures. There was an abscess in the head of each humerus, a pyarthrosis, and a small focus in the myocardium.

(3) *Reptiles.*

(*a*) Water-pilot, No. 412/27, with salpingitis, and abscesses in the liver, the lung, and in the myocardium.

(*b*) Bull-Snake, *Coluber melanoleucus*, No. 452/27. There was a fairly heavy infection with helminths, some being found actually in the portal vein itself. There were several small abscesses scattered in the liver, and at the upper level of this organ a mass of creamy and partly inspissated pus involving the parietal peritoneum and extending into the fascia and intercostal muscles. The spleen contained a large abscess and there were a few small purulent foci in the kidneys.

6. NEOPLASMS.

Below is a list of the animals in which new growths have been encountered during the year. One or two only (marked with an asterisk) are described in any detail as the subject is a large and important one, and it is intended to make it a question for treating in a special paper subsequently.

(1) *Mammals.*

(*a*) Pardine Genet, *Genetta pardina*, No. 298/27. Malignant fibro-adenoma, or adeno-carcinoma, of the thyroid.

(*b*) Common Wolf, *Canis lupus*, No. 299/27. Squamous epithelioma of the tonsil. A separate paper describing this has already been offered to the Publication Committee of the Society.

(*c*) *Weeper Capuchin, *Cebus apella*, No. 359/27. Carcinoma, ? mesothelioma, widespread.

(*d*) Eland, *Taurotragus oryx*, No. 362/27. Sarcoma of lungs.

(*e*) Raccoon, *Procyon lotor*, No. 839/27. Growth of thyroid with secondary metastases in lungs.

(*f*) *Crowned Duiker, *Sylvicapra coronata*, No. 192/27. Growth of mediastinum, with secondary deposits in the lungs.

(2) *Birds.*

(*a*) *White-necked Stork, *Dissoura episcopus*, No. 32/27. Neoplasm in Myocardium with secondary invasion of lungs, probably endothelioma.
(*b*) *Budgerigar, *Melopsittacus undulatus*, No. 156/27. Hypernephroma of right kidney.
(*c*) *Budgerigar, No. 245/27. Hypernephroma of left kidney.
(*d*) *Budgerigar, No. 403/27. ? Neoplasm of peritoneum.
(*e*) *Budgerigar, No. 593/27. Fibro-adenoma (? carcinoma) of ovary.
(*f*) Rüppell's Long-tailed Glossy Starling, *Lamprotornus purpuropterus*, No. 795/27. Neoplasm of liver, ? melanotic sarcoma.

(3) *Reptiles.*

(*a*) *Tigrine Frog, *Rana tigrina*, No. 30/27. Adenoma and mycosis.
(*b*) *Moccasin, *Ancistrodon piscivorus*, No. 76/27. Malignant adenoma (duct adenoma) of liver.
(*c*) Galeated Pentonyx, *Pelomedusa galeata*, No. 91/27. Neoplasm of right ovary.
(*d*) Elegant Terrapin, *Chrysemys elegans*, No. 93/27. Sarcoma of femur.
(*e*) Exanthematic Monitor, *Varanus exanthematicus*, No. 209/27. Neoplasm of liver.
(*f*) Nilotic Monitor, *Varanus niloticus*, No. 565/27. Growth of liver.
(*g*) Gigantic Cyclagras, *Cyclagras gigas*, No. 751/27. Sarcoma of neck (spindle-cell).

1. The Weeper Capuchin, *Cebus apella*, No. 359/27, presented a remarkable pathological condition. It had been in the Gardens for seven months, and during the last three weeks of its life had been in the Sanatorium on account of emaciation and progressing weakness; there had been no cough. An autopsy was performed within an hour or so of death. On opening the body the *right pleura* was found to be adherent to the inner aspect of the ribs throughout its whole extent, and there was a little blood-stained fluid, 2 ozs. or so only, in the pleural cavity. The *right lung* was large and filled the right side of the thorax, and even encroached beyond the middle line. It was largely occupied by innumerable semi-translucent nodules of gristly consistence, each the size of a small pea, but in some parts coalescing to form a mass as large as a filbert. The upper part was firmly fixed to the upper ribs and clavicle. In the *left pleural cavity* was turbid, but not blood-stained, fluid; the *left lung* was thrust back into the costo-vertebral angle, but was also infiltrated densely with nodules similar to those in the right lung. The right side of the *diaphragm* was densely infiltrated, and the *pericardium* showed several deposits on the surface and extending through the membrane to the interior, but none were seen on or in the heart itself. There were scattered deposits on the inner aspects of the ribs on both sides. With the exception of the kidneys and adrenals, the abdominal viscera were free from disease. The upper pole of the *right kidney* was enlarged to the size of a golf-ball, with a bossed surface due to the many nodules of growth; the *left kidney*

was but little more than the normal size, but within it, on the antero-lateral aspect, was a deposit, similar to the others, the size of a large pea; the *adrenals* were large and prominent, and in the left were small whitish deposits. There was infiltration of the glands in various situations, namely at the hilus of the lungs, the sternal, infra-clavicular, vertebral, diaphragmatic, and lumbar glands. A study of the sections reveals the condition to be a highly malignant growth.

I am indebted to Dr. J. Beattie, late Anatomist to the Society, for the following remarks on the anatomical distribution of the lesions:—

Primary lesion. Upper pole of the right kidney. Primary spread to lungs *viâ* the renal veins, inferior vena cava, and pulmonary arteries. These are the *first* crop of *secondary metastases* (in lungs). Spread from lungs (second crop of metastases): (*a*) to hilus glands; (*b*) through pleural adhesions to the subpleural plexus under the mediastinal pleura. *Tertiary lesions* (third crop) found in the following sites: (*a*) in sternal glands and in sternal lymphatic vessels, and in the infra-clavicular glands; (*b*) in vertebral lymphatic glands; (*c*) in diaphragmatic glands (from the mediastinal subpleural plexus). *Quaternary-lesions* (fourth crop): (*a*) into superior surface of the diaphragm and thence to the lumbar glands; (*b*) by either retrograde lymphatic flow to the left kidney or by infection through the blood-stream (unlikely).

2. Crowned Duiker, *Sylvicapra coronata*, No. 192/27. At the upper part of the thorax was a large mass filling the *anterior mediastinum*, yellowish-white in colour. It lay between the pleural sacs, but adherent to both. The upper lobe of the *right lung* was solid with tumour-mass, extending directly into the growth in the mediastinum. The middle lobe was marbled with growth which seems to have extended by way of the bronchi, and the lowest lobe was heavily infiltrated. There was no direct extension of the central tumour into the *left lung*, but secondary deposits were present in it also, having apparently gained entrance along the bronchi. Both lobes were affected, but the upper more than the lower. The *pericardium* was adherent to the under surface of the mediastinal tumour, and was thickened and infiltrated. The thymus was not obviously connected with the main tumour. The bronchial glands were infiltrated, as were also the internal mammary, all being enlarged, whitish in colour, and hard.

Sections showed the growth to be a *Streptothrix*. Extension would seem to have taken place at first by contiguous spread and later by way of the bronchi.

3. The White-necked Stork, No. 32/27, showed a white deposit in the myocardium involving both the right and the left ventricles anteriorly. It extended throughout the wall of the left

ventricle to the endocardium, and when the cavity was opened, there was seen to be an excrescence projecting into it and several smaller, more sessile, deposits, and scattered in the thickness of the myocardium were others. There were two small focal deposits in the lungs. Microscopically, the tissue was made up of spindle-cells adjacent to and invading the heart-muscle, and there were aggregations of larger cells with a vacuolated cytoplasm. Intermixed were small, hyaline, and granular masses, which were, perhaps, degenerating muscle-fibres. The deposit seemed to be hardly cellular enough to be a sarcoma, but rather of an endotheliomatous (mesotheliomatous) type. Moreover, in the secondary deposits in the lung the aggregated cells were chiefly peri-arterial, and the endothelium had a palisade-like arrangement with surrounding extravasation and cellular proliferation—in short, a perithelioma.

4. The four Budgerigars may be considered together:—

(*a*) The first, No. 156/27, had a tumour the size of a small cherry, pinkish-yellow in colour at the upper pole of the right kidney, attached internally to the testicle and externally to the kidney. It may have been an adenoma of the adrenal, or a hypernephroma of the kidney, as in its growth it had obliterated the adrenal gland; its structure is that of a hypernephroma.

(*b*) The second, No. 245/27, was very similar, but on the other side. There was a yellowish mass, as large as a pea, to the left of the left testis and adherent to the left kidney in the region of the upper pole. It had the same structure as the last and infiltrated into the kidney tissue.

(*c*) In the third, No. 403/27, the peritoneum was thickened and adherent to the abdominal wall, and there was bloody fluid in the peritoneal cavity. Lying in the cavity was a large tumour, the size of a walnut, which was of varied consistence, part being cystic, part gelatinous, and part solid. Microscopically, at the outer edge was seen what appeared to be the epithelium lining the peritoneum, while the interior seemed to consist entirely of blood, clotted and broken down. The condition may have been an organizing or broken-down hæmorrhage in the peritoneum or hæmorrhage into a peritoneal cyst.

(*d*) The fourth, No. 593/27, presented a nodular tumour, partly solid, partly cystic, the whole being as large as a walnut, in the ovary. There was a hæmorrhage in the peritoneum over the left half of the growth. Microscopically, it was seen to be a fibro-adenoma (? carcinomatous). Death was due to pneumonia. No metastases were found.

5. Tigrine Frog, No. 30/37. This has already been mentioned under the heading of Mycosis, as the first instance of infection of this species by *Monilia batrachea*. The kidneys were fused together in the middle line, and on the left surface was a tumour 1·4 cm. in diameter, rough and granular, infiltrating into the tissue of the kidney. In the lungs there were several small nodular deposits, and in the liver were many greyish translucent foci which were thought to be perhaps helminthic. In the portions taken for microscopical examination, there was very little normal renal tissue to be seen, the structure being that of an adenoma, while hyphæ of the mould were present in some of the tubules which survived. In the lung sections a similar development was present, together with hyphæ, and many alveoli were filled with growth. The tissue in the lungs strongly resembled the renal growth, but in parts the alveolar arrangement of the cells may have been the result of reaction to hyphal growth and to enclosure within the walls of the pulmonary alveoli. The liver sections showed only granulomatous tissue, and much of it necrotic, without hyphæ.

A possible explanation is the following:—Infection by the mould in the kidney causing irritation and resulting adenoma-like growth, whence secondary deposits had occurred in the lungs; or the mycotic infection in the lungs may perhaps have been primary there, or at least independent, and reaction to the hyphæ and enclosure in the alveoli have produced the resemblance, as mentioned above, to the gland-like growth. This may possibly account for some, but not for all, since some of the alveolar cells in the lung are cubical, like those in the renal part of the tumour.

6. Notes on some East African Invertebrates collected in 1926. By ARTHUR LOVERIDGE, C.M.Z.S.

[Received August 5, 1927: Read November 15, 1927.]

The following observations were made when I was engaged on a comparative study of the herpetological faunæ of the Uluguru and Usambara Mountains in Tanganyika Territory on behalf of the Museum of Comparative Zoology, Cambridge, Mass. To these have been added half a dozen earlier unpublished notes.

With the exception of Dar es Salaam and the few places mentioned in the earlier notes, all localities mentioned are in one or other of these mountain-ranges, their approximate altitude being as follows:—

Uluguru Mountains.		Usambara Mountains.	
Mkangazi,	3000 feet.	Amani,	3000 feet.
Mkarazi,	1500 „	Bumbuli,	2000 „
Vituri,	2000 „	Derema,	3000 „
		Lutindi,	4000 „
		Phillipshof,	5500 „

My grateful thanks are due to Messrs. Nathan Banks, Preston Clark, W. J. Clench, H. G. Dyar, S. Hirst, and Prof. W. M. Wheeler for carrying out identifications of the species in their own particular groups.

PHEIDOLE MEGACEPHALA var. PUNCTULATA Mayr.

My tent appears to have been pitched right above a nest of these annoying little ants, which explore every corner in search of the edible. In the afternoon I disembowelled a snake, the internal organs lying on a sheet of paper on my table. In a matter of seconds—or so it seemed to me—the news had spread, and a column, composed of two or three ants abreast, were streaming from the table on my left to the table on which the remains were; the two tables were of the same height and in contact with one another. I drew my table an inch away and watched to see what the ants would do. One after another paused for a fraction of a second on reaching the brink of the precipice and then leaped off—there was no question of falling; they actually jumped. Having watched fifty or thereabouts play "follow my leader" in this way, I swept up the rest of the column and gave them to the frogs (Mkarazi, 21. x. 1926).

TETTIGONIA sp. immature.

In the Lushoto–Phillipshof area of the Western Usambaras one is often surprised at heavy drops as of dew falling from the trees. This occurs on bright sunny days just as much as on overclouded ones. The cause of the phenomena is a larval bug called by the Wasumbara natives *kidodwe*. It is a little greyish-green creature with black markings on the head and thoracic region. These larvæ assemble in groups, composed of about a score of individuals, on the twigs and smaller branches of the *Albisia*-trees to feed by suction on its juices. They envelop themselves in a mass of froth, comparable to the "cuckoo-spit" of milder climates, and it is from this that the drops form and precipitate. Mr. D. K. S. Grant, Chief Conservator of Forests in the Territory, informs me that the tree from which they were collected, and which I pointed out to him, is probably *Albisia fastidiata* (Phillipshof, 28. xii. 1926).

TEFFLUS OBLONGICOLLIS Sternberg.

While walking up the road behind me this morning, my wife called out for the forceps, with which to pick up a large Carabid known as *dinindi* to the Wasumbara. I suggested that it was quite harmless and that she should pick it up in her fingers. However, as she threatened to let it go if I did not produce the forceps, I repented and returned to pick it up myself. She had headed it off with a stick, and it had come to rest among some dead leaves drifted against the bank, or cutting, on the mountain side of the terraced roadway. As I approached, my hand with the forceps, it slightly tilted its abdomen and discharged some acid on the dorsal aspect of my wrist (which was a foot from the beetle) and on the inner aspect of my fore arm at the elbow (which was quite twenty inches from the insect). The burning of the acid on my wrist was slight, but where four drops fell on my arm it caused severe pain; the four spots became white immediately and later turned red (Amani, 20. xi. 1926).

I have since caught several more of these black-and-white beetles, and it is only occasionally that they use this defence. The irritation lasted about an hour; the red spots remained four days, and one has not entirely disappeared at the time of writing (Amani, 27. xi. 1926).

LIMACODID LARVA, probably of the Genus SETORA.

A native brought me an extraordinarily bizarre and handsome caterpillar which the Wasumbara know well and call *chawaghe*. It is just over an inch (thirty millimetres) in length; the back and sides are at right angles to each other, and the tail-end by descending abruptly contributes to the box-like outline of the creature. On the back of the head are two short horns, and these, like the other horns about to be described, give off black bristles which are banded with white near the tips; another pair arise on the first segment and point forwards; a second outward and backward pair from the second segment; a third backward-pointing pair on last segment—all of these are bright Cambridge blue. In the centre of the back are a series of diamond-shaped green patches bounded by yellow lines. The rest of the geometrically-planned pattern is composed of triangular green patches; laterally there is a dark blue line bounded by a red one and a yellow one; the sides are yellow, with more or less quadrilateral green patches; below these are ten pairs (*i. e.* ten on each side or rear) of shorter greenish bristle-bearing horns similar in size and appearance to the first pair (Amani, 25. xi. 1926).

When out in the forest this morning one of the natives was severely stung on the foot by the spines of this caterpillar, which he brushed against or trod on in the undergrowth. Other natives informed me that its stinging possibilities are well known, and in consequence they avoid interfering with it (Derema, 2. xii. 1926)

ACANTHOSPHINX GUSSFELDTI (Aurivillius).

A native youngster brought me a fine moth measuring six and a half inches across the wings (164 mm.); naturally it was much rubbed by handling, but the ochre-coloured antennæ were intact; the thorax was covered with scales like black velvet, the wings a brownish-grey anteriorly and olive posteriorly. It was a female, the abdomen being distended with many eggs. The interesting thing about the insect was its legs. The child dropped it on my table, and twice I picked it up and twice I dropped it, for its legs were armed with thorn-like spines! The front pair were unarmed, the middle pair carried two spines apiece, and the posterior pair three spines, the longest of which measured seven millimetres, or nearly three-tenths of an inch, very formidable weapons when pressed into unwary fingers (Mkangazi, 20. x. 1926).

ATTIDÆ.

On my breakfast table this morning I noticed a suspicious-looking "ant" waving palpi! Closer investigation revealed that it was a spider. A second individual was descending from the jam jar and a third was on a book. Placing them in a tube I also put in a bead of jam, to which one of the spiders ran, mounted it with his fore legs, and seemed to be feeding. In approaching a magnifying-glass to see if this were really so, I scared it, and never saw one of them return to the jam the whole morning, though I kept the tube under observation as I was writing. A diminutive tineid moth and an ordinary housefly introduced from time to time only frightened the spider, who scurried *away* from the meal I had provided! (Vituri, 31. x. 1926).

BABYCURUS GIGAS Kraepelin.

This large scorpion, called *kisusi* in Kisumbara, was the only scorpion met with in the Uluguru and Usambara Mountains. It is more abundant in the latter than in the former, and most of the specimens were collected at Amani. They were almost always found under the bark of standing or fallen trees or in cavities in the decayed trunks. At Nyange a native was returning with several of them in a bag when he allowed the bag to brush against his bare leg. The resulting sting, though momentarily severe, did not appear to trouble him much after the first day.

ISOMETRUS MACULATUS De Geer.

This little scorpion was found to be extraordinarily abundant in, and under, piles of old palm-leaf thatching, of which one sees so much on the outskirts of villages. About thirty scorpions were seen in a single heap. One of these scorpions carried nine very diminutive and pallid offspring neatly packed upon her back. Salimu picked up nearly all our specimens with his bare fingers; the majority he took up by the tail, but he would often clap a hand down on a fleeing scorpion or grab at one anyway he could. I saw him stung about the finger nails several times. He said that he felt the stings, but they were of no account as he had previously been inoculated against them! The other natives were very cautious in handling these scorpions (1–3 miles south of Dar es Salaam, 6. xi. 1926).

PHRYNISCUS BACILLIFER Gerst.

In the process of demolishing a large termite-hill we unearthed a big female whip-scorpion. Her abdomen was concave as viewed from below, but this concavity was occupied by a roundish membrane. This membrane was apparently extruded from a small aperture on the anterior ventral surface of the abdomen, and was much distended with thirty-one eggs, having the appearance of white millet (Mkata Plains, near Kkata River, 30. viii. 21).

SCOLOPENDRA MORSITANS Linnæus.

In clearing some leaves from a gutter at Morogoro a native gathered up one of these handsome centipedes and got bitten on the hand. The pain was intense at first, but by the following day the man did not appear to suffer much inconvenience. I recall how at daybreak one hot and breathless morning at Frere Town I went out to the verandah and sank into a Madeira chair only to rise as promptly, for a *morsitans* emerged from one of the arms and began hurrying about in search of a quieter retreat. Elsewhere specimens were collected at Moshi, Kilosa, Dar es Salaam, and Lumbo (*v. d.* 1918–1921).

ETHMOSTIGMUS TRIGONOPODUS Leach.

One of the commonest species, particularly in evidence after the first rains of the seasons. Specimens six inches in length were often collected, and I found it a difficult business to pick them up with a five-inch forceps; you can both see and hear their big jaws champing on the metal. The biggest I have seen (though possibly it was *Trachycormocephalis mirabilis*, which was also collected in this camp) was at Longido West, 27.i.16, when I was roused one night to capture the creature, which was scurrying over the "ceiling" of someone's tent. I succeeded in getting it into the killing-bottle, but it was out again before I could push the cork in place. As it made good its escape, its size could only be estimated; this we agreed was ten inches in length by half an inch in breadth. Elsewhere specimens were collected at Mbunyi, Moshi, Morogoro, Kilosa, Simbo, Izikisia, and Lumbo.

ALIPES GRANDIDIERI Lucas.

The handsome violet Raquet-tailed Centipede, called *luge* by the Wasumbara, is scarce in the Uluguru Mountains but very abundant on Mt. Bomori (Bomoli) at Amani, in the Usambaras. It is well distributed through the surrounding country, where it was found in large rotting sections of tree-trunks.

The adult is plumbeous with violet-coloured legs, but its chief claim to distinction is a pair of large leaf-like or racquet-shaped caudal appendages each having a splash of violet on its otherwise semi-transparent brownish surface; there is a reddish mark near the base of the leaf, and sometimes the colouring is suggestive of eye-spots. The antennæ are purplish or deep violet. It has been said that the appendages are waved to and fro during the progress of the centipede, in order to distract the attention of birds who might thus be led to attack the least important end. To test this I liberated several centipedes on the road, but the appendages were carried at an obtuse angle and not moved at all. In marked contrast is its behaviour if held down or arrested in its walk; then they are violently agitated, as the creature wriggles and bites in desperate efforts to free itself.

Many females were taken carrying their eggs or young. They were found resting in cavities in the logs and holding the eggs or young with the posterior middle pairs of legs; in walking this necessitated certain segments of the body being arched. Not infrequently a second centipede, presumably the male, was found in the same cavity as the egg-holding female. The eggs, which were three millimetres in diameter, have the appearance of little globules of pale amber; their numbers vary considerably—in one instance a female carried twenty-four, in another seventy. The young when hatched are perfectly white and show no trace of the leaf-like appendages; these young lie parallel with the mother's body and form quite a considerable bundle, as fifty-five were removed from one female on November 24th. Thirty-seven were taken from another female on the same date; these were more advanced and showed slight violet tinting and leaf-like appendages. My native collectors brought in eight others the same day which were violet-coloured, but whether taken off the mother, or only with her, I cannot say (Amani, 24.xi.1926).

GEOPHILIDÆ.

Two slender geophilids outside my tent attracted attention by the very strong phosphorescent trail which they left; their glands literally spilt phosphorus on the forceps when picked up. Though only an eighth of an inch in breadth, one measured seven inches in length (Kibakwe, 9.ii.1923).

The first heavy rains for many months fell yesterday, and this morning two geophilids were found partially buried in the sandy road; each was holding a large and still struggling termite (Kikuyu, 10.ii.1923).

Very numerous under stones between Mpanira and Kidengo, ii.1923.

POLYDESMIDÆ.

When several of these large brown polydesmids (*Orodesmus ornatus* Cook ♀, and *Orodesmus* spec. ♀) are placed in a cyanide bottle their exudations smell strongly like crushed laurel leaves (Lutindi, 10.xii.1926).

SPIROSTREPTUS.

When taken off a tree-trunk this large black millipede exuded a fluid which stained my fingers yellow and smelt like nitric acid most powerfully (foot of Mt. Lutindi, 11.xii.1926).

ACHATINA RANDABELI Bourguignat.

In cleaning one of these mollusks (M.C.Z., No. 53211), picked up to-day, I found in the apex of the shell eleven eggs of a pale lemon-yellow colour and each measuring 6 × 4 mm. (Kilosa, 20.vii.1921).

ACHATINA ZANZIBARICA IHOTELLERI Bourguignat.

This species of giant snail is viviparous, for I found one dead upon the path with many young snails dead within and around its shell (Amani, 22.xi.1926).

If further proof were necessary, it was furnished to-day by a native who, in carrying home three of these snails for me, broke one and thus liberated seventy-four young snails, each of whose shells measured about 10 × 8 mm. (Amani, 27.xi.1926).

ACHATINA ZANZIBARICA IHOTELLERII Bourguignat.

In walking through the forest here we have been struck by the number of large snails, *koswe* as they are called by the Wasumbara, lying on the paths. Their shells being smashed, there are liberated a great many bright chrome-coloured, hard-shelled eggs measuring 10 × 7 mm. each. It seems probable that the snails had fallen from the branches some sixty feet overhead; and as only one of eight specimens seen in this afternoon's walk was without eggs, it appears possible that the heavily-laden females misjudge their adhesiveness to carry the weight of eggs, thus meeting with an untimely end.

That this is not the normal way for the eggs to be liberated (as one conversant with native stories as to the birth of chameleons might be led to suggest) is proved by the fact that we found several batches of the eggs deposited in moist situations beside, and almost beneath, fallen tree-trunks. One batch of eggs, strewn around the remains of a broken shell on the path, was found to number slightly over one hundred and four individuals (as some were smashed, the precise number could not be ascertained). That these giant snails have not been broken by some bird or beast of prey is to be argued from the fact that the flesh is not molested, but provides food for the hordes of ants which attack every helpless or dead creature in the forest. There remains the possibility that they are wantonly thrown down by colobus monkey, or hornbill, all of which are plentiful in the forest (Amani, 21. xi. 1926).

Mr. W. J. Clench, who has determined these shells, adds the following note:—

Pilsbry* reports that the "*Achatinæ* are oviparous; their eggs are numerous, as many as one hundred and ninety-six having been seen to be deposited by one individual." The two cases recorded above probably indicate an oviparous condition, at least existent in this species of *Achatina*. The usual method is perhaps the laying of the eggs before hatching, only an occasional individual producing the young alive. It is quite probable that these eggs hatch very soon after being laid, though I have failed to find any notes regarding this matter; perhaps the above notes pertain to individuals that were unable to find suitable places to deposit the eggs before hatching.

---

* Pilsbry, H. A., 1919, Bulletin. Am. Mus. Nat. Hist. vol. xl. art. 1, p. 60.

7. Notes on Oriental Dragonflies [Odonata], with Descriptions of New Species. By the late Mr. H. CAMPION and by F. F. LAIDLAW, F.Z.S.

[Received November 9, 1927: Read February 7, 1928.]

(Text-figures 1–3.)

CONTENTS.

		Page
I.	Introduction	129
II.	Notes and Descriptions of New Species	129

I. Introduction.

Amongst some manuscript notes of the late Mr. H. Campion were descriptions of two new species of dragonflies from Luzon, together with admirable wing-photos by Mr. F. W. Campion. The descriptions were drawn up with the care and accuracy which was so characteristic of my friend, and it seems to me that they ought to be published. I have arranged them, as they were not in suitable form for printing, and with them offer some notes of my own on species which are new or otherwise of interest.

II. Notes, and Descriptions of New Species.

Tetracanthagyna bakeri, sp. n., Campion (MSS.).
Mesogomphus henryi, sp. n.
Procordulia heterodoxa (Selys).
Macromia moorei malayana, subsp. n.
Orolestes wallacei (Kirby).
Calicnemis chaseni, sp. n.
Teinobasis nigra, sp. n., Campion (MSS.).

ANISOPTERA.

ÆSCHNIDÆ.

TETRACANTHAGYNA BAKERI Campion MSS., sp. n. (Text-fig. 1.)

1 ♂ (holotype), Mt. Makiling, Luzon (*C. F. Baker*).

Length of abdomen 60+7·5 mm., of hind wing 60 mm.

Labium, labrum, clypeus, and antennæ pale reddish brown; frons brownish yellow; anterior ridge on frons black, the blackness extending over the superior surface of the frons in the form of an ill-defined triangular mark. Vertex reddish brown.

Prothorax pale yellow.

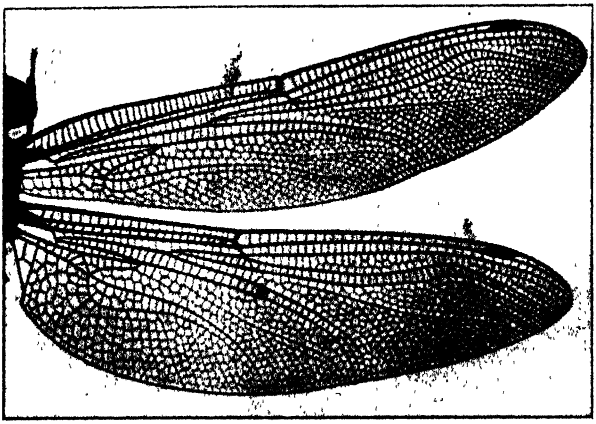
Meso-metathorax rather dark reddish brown, without pale stripes or other markings.

Legs bright reddish brown ; tarsal claws blackish.

Abdomen very dark reddish brown, tending to become black towards the terminal segments, without pale markings of any kind. Segments 8 and 9 without any apical spines.

Anal appendages. Upper pair black, as long as abdominal segments 9 and 10 together, each in dorsal view narrow at base, and gradually becoming wider until just before the apex, which ends in a short acute point directed slightly outwards; in lateral view rather wavy, considerably thickened a little beyond the extremity of the lower appendage, without any ventral spine.

Text-figure 1.



Wings of holotype male *Tetracanthagyna bakeri.* (F. W. Campion photo.)

Lower appendage black tinged with red, truncate and slightly bifid at apex, a little more than half as long as the upper pair, gently curved upwards from base to apex.

Wings without markings, except for a trace of dark brown in the costal and subcostal spaces at the base of each wing.

Main longitudinal veins somewhat reddish at base, venation otherwise nutmeg-brown. Pterostigma 3·5 mm. long, not braced.

Anal loop of hind wing containing 13–15 cells, membranule whitish. Area between Cu_1 and Cu_2 in fore wing with one row of cells at base.

Five rows of cells between *Rs* and *Rspl* on fore wing, four to five rows between M_4 and *Mspl* at widest point. Anal triangle 3-celled. Triangle of fore wing with 8–9 cells, of hind wing with 7–8 cells. All four sub-triangles 2-celled. Supra-triangles $\frac{10, 11}{7, 8}$.

1 ♂, Mt. Makiling, Luzon (*Baker*, 21199). Paratype.

Length of abdomen 58+8 mm., of hind wing 58·5.

Pterostigma 3·5 mm., dark reddish brown. The darker pterostigma indicates that this specimen is more fully adult than the holotype. The venation is reddish throughout. Otherwise the specimen agrees very closely with the type.

A third specimen from the same locality as the two preceding likewise conforms closely to the description of the type.

This fine new species, whose discovery extends the range of the genus to the Philippine Islands, is very distinct from other members of the genus, but at the same time falls within the generic definition without any difficulty.

By its uncoloured wings it differs from *plagiata*, *vittata*, *brunnea*, and *degorsi*, and by the unmarked thorax from *plagiata*, *vittata*, and *waterhousei*. In size it agrees fairly well with *degorsi* and *waterhousei*.

The female is unknown.

[It may be remarked that the male of *brunnea* is also unknown, and if, as is possible, that sex has colourless wings and is smaller than the female to the same degree proportionately as are males of the other species (the female *brunnea* has the hind wing 67 mm. long), then the male *brunnea* may prove to be very much like the male *bakeri*.]

Holotype ♂ in British Museum.

Paratypes ♂ in British Museum and ♂ sent to U.S. National Museum, Washington.

GOMPHIDÆ.

MESOGOMPHUS HENRYI, sp. n.

4 ♂ ♂, 1 ♀, Woodside, Urugalla, Ceylon, 3000 ft., 15. iv. 24. "Sits on stones in stream."

♂. Length of abdomen 30+3·5 mm., of hind wing 25 mm., pterostigma 4 mm.

Colouring black varied with yellowish green.

Head. Labrum yellow, with a black triangular mark at its base, the apex of the triangle directed forward. Anteclypeus yellow, post-clypeus black. Genæ yellow. Frons, vertical part black, horizontal part black, with a pair of transverse-oval yellow spots. Vertex black.

Prothorax. Dorsal surface entirely black.

Meso-metathorax black, marked with greenish yellow as follows: A mesothoracic collar, interrupted in the middle line. A pair of narrow, oblong-oval, dorsal spots not meeting the collar, and running obliquely outward and forward, a minute humeral spot above and to the outside of these on either side. The meso- and metepimerites largely yellow, with a broad black band covering the metepisternite and extending a little on either side of it. Hinder margins of metepimerite black. Legs black, outer surface of basal half of femora marked with yellow.

Abdomen black, segments 1 and 2 with yellow lateral markings, which include the auricles. The second segment has also a narrow, longitudinal, mid-dorsal band of yellow. Segments 3–7 with lateral basal markings of the same colour; those on 4-6 small and triangular, on 3 and 7 extending for fully the basal half of the segment, and each divided into two by a fine transverse line of black.

Segments 8, 9, 10 almost entirely black; in one specimen there is an obscure mottling of brown on the exfoliation of 8–9, which are otherwise entirely black, except the ventral surface of 10 which is dark brown-black.

Anal appendages identical in shape with those of *M. lineatus* (and of other males of the genus). Upper pair formed rather like a pair of chamois-horns, olive-brown, tinged with black at the base; lower appendage much shorter, strongly curved and deeply cleft, black or very dark brown.

Costal nerve finely lined with yellow as far as the pterostigma. Fore wings with 12 antenodal and 7 post-nodal cross-nerves.

♀. Length of abdomen 29 mm., of hind wing 26·5 mm.

Wing with a smoky tinge.

Colouring as in the male. Abdomen slender, its three apical segments entirely black.

Vulvar scale short, about one-half the length of the ninth segment, deeply cleft.

1 ♂, 1 ♀. Holotype and allotype, in the British Museum. 2 ♂ ♂ paratypes returned to the Colombo Museum. 1 ♂ paratype in my own collection.

This fine addition to the dragonfly fauna of Ceylon is closely allied to *M. risi* Fraser. It differs in its larger size, narrower dorsal thoracic markings, and black vertex, as well as in having the anal appendages yellowish brown, whilst in *risi* they are black marked with yellow at the base.

Another allied species, *M. capricornis* (Förster) from Singapore, has the dorsal thoracic spots more roundly oval, the labrum and clypeus entirely yellow, the exfoliation of the ninth segment of the abdomen bright orange-yellow, and the anal appendages jet-black.

The terminal segments of the abdomen and the anal appendages of the males of all the species of the genus are very similar in structure and appearance.

LIBELLULIDÆ.

CORDULIINÆ.

PROCORDULIA HETERODOXA (de Selys).

1 ♂, 1 ♀, Mt. Makiling, Luzon (*Baker*).

Examination of this pair makes it fairly evident that the species is not a true *Somatochlora* and can be referred without much difficulty to the present genus.

The "*internal triangle*" of the hind wing is absent in both the specimens before me, and also in the female figured by Martin (*loc. cit.*).

Venationally *heterodoxa* differs a little from other species of *Procordulia* in having an accessory "bridge cross-nerve."

It differs also in the shape of the anal appendages of the male, which are long and have the upper pair decidedly more like those of some species of *Somatochlora* than those of *Procordulia.*

In general appearance this beautiful species resembles rather closely *P. sumbawana* (Förster), which is geographically its nearest neighbour—this latter, of which I have been able to examine two males from Celebes in Mr. Williamson's collection, is a true *Procordulia*, and its recorded range includes Java, Lombok, Sumbawa, and Celebes. This species was also described as a *Somatochlora* in the first instance.

It is possible that *heterodoxa* may ultimately require the creation of a distinct genus to hold it. This genus would be characterised by the absence of an internal triangle in the hind wings, the presence of an accessory bridge-nerve, and the brilliant metallic colouring of the body, with the thorax unmarked. The upper anal appendages of the male long, straight, and bluntly pointed, and the second tibia without keel. (See Walker, University of Toronto Studies, Biological Series, No. 26, p. 16.)

MACROMIA MOOREI MALAYANA, subsp. n.*

1 ♂, L. Tamang, Pahang, 13. vi. 23 (*F. N. Chasen*). (Holotype; deposited in the British Museum.)

Length of abdomen 44 + 2·5 mm., of hind wing 43 mm.

Head. Upper lip, clypeus, frons, and occiput reddish brown, the horizontal part of the frons and the vertex with metallic-green reflex.

Prothorax reddish brown.

Meso-metathorax reddish brown, with a lateral yellow stripe covering the spiracle and lying along the line of the first lateral suture. On either side of this yellow line the lateral surface is strongly tinged with metallic green, whilst the upper half of the dorsum has a distinct, though less strong, tinge of the same colour. The yellow lateral line is continuous over the postnotum.

Abdomen black, without green metallic reflex. First segment brownish yellow. Segments 3–5 with yellow lunular ring; 7 with a yellow ring covering its basal third, and prolonged a little in the mid-dorsal line.

The tenth segment has a longitudinal mid-dorsal ridge, on either side of which near its proximal end there is a very minute tubercle.

Legs black.

Anal appendages black. Upper pair each with a small median externo-lateral tooth. Lower appendage equals upper in length.

---

* *Cf. M. trituberculata* Fraser.

Wings. 14 antenodals, 9 post-nodals on fore wing, otherwise as in typical race.

Genital structures of second abdominal segment. Apparently closely similar to those of typical race, but the specimen is crushed and exact details cannot be made out.

Distinguished from the typical race, which occurs in Assam, by the absence of yellow markings on the sixth abdominal segment, less extensive yellow on the seventh segment, and absence of brown markings on segments 8, 9, 10, as well as by the black colour of the anal appendages, which in typical *moorei* are brown.

ZYGOPTERA.

SYNLESTIDÆ.

OROLESTES WALLACEI Kirby.

Lestes wallacei Kirby, Proc. Zool. Soc. London, 1889, pp. 302–303.

Lestes ridleyi Laidlaw, Proc. Zool. Soc. London, 1902, p. 92.

Lestes sp., Laidlaw, Rec. Ind. Mus. xix. 1920, pp. 148–149, fig. 1.

2 ♂♂.

I have compared these specimens with Kirby's type (♀) in the British Museum, and am satisfied as to the correctness of the synonymy quoted above. Also, by the kindness of Col. Fraser, who has examined the type of *Orolestes selysi* in the McLachlan collection, I have been able to determine that the present species is beyond doubt congeneric with McLachlan's species, and must therefore be referred to the genus *Orolestes*.

Orolestes wallacei has not the richly pigmented wings of *O. selysi*, but an examination of the wing-photo taken for me by Mr. F. W. Campion will show that the whole costal area of both pairs of wings is definitely, though not strongly, tinged with grey-brown (see Laidlaw, Rec. Ind. Mus., *supra*, text-fig. 1). The wings altogether have a more "smoky" appearance than is the case in Oriental species of *Lestes* with which I am acquainted. In younger males, however, and in the female this trace of pigmentation is absent or very little evident, and even in the adult male figured such evidence as it affords in support of the reference of the species to *Orolestes* was overlooked by me.

In discussing the venation of the specimen figured, I suggested that there was a slight error in McLachlan's description of the quadrilateral of the genotype; and I find from Col. Fraser that my surmise was correct. I propose to define the genus as follows:—

A genus of the Synlestidæ in which the adult males of the known species have wings with some degree of colouring. The wings are petiolated to the level of *Ac*, which lies nearer the level of the first than of the second antenodal. *Rs* rises about one cell distal to point of origin of M_3; an oblique vein usually present. Venation very rectangular, except about the supplementary sectors. These are developed between M_{1a} and M_2, between M_2 and *Rs*, and between *Rs* and M_3. Quadrilateral with its anal side twice the length of the costal side. Pterostigma large, about four times as long as broad. Abdomen relatively long and slender.

Distribution. Assam, Tonkin, Malay Peninsula, Borneo.

I do not doubt but that the larva described by Needham (Entomol. News, xxii. 1911, pp. 342–344, pl. xi. figs. 1–4) is to be ascribed to *Orolestes* and in all probability to *selysi*. It is distinctly Synlestine in character, and not unlike that of *Megalestes major* Selys, of which I have given a short account (Rec. Ind. Mus. xix. 1920, pp. 185–187, text-figs. 1, 2). I have discussed these larvæ with Dr. Tillyard, who agrees that they must be regarded as belonging to species of Synlestidæ.

The genus *Orolestes* simulates *Lestes*, perhaps, more closely than does even *Megalestes* as regards its venation. But the regular rectangular character of the venation is enough to put one on one's guard, though it is true that both Kirby and myself were not sufficiently impressed thereby to refer the species otherwise than to *Lestes* in the first instance.

Three species of the genus *Orolestes* have been described. The males may be distinguished as follows:—

I. Wings coloured in parts with deep brown-black.	
a. Pigmented area extends from nodus to within one or two cells of the pterostigma, its distal margin crossing the wing transversely at right angles to the long axis of the wing. 19-20 post-nodal nerves. Length of hind-wing about 37·5 mm. .	*O. selysi* McL.
b. On all four wings a transverse band of dark brown beginning at the nodus and extending to a point about 8 cells distal to it, widening posteriorly so as to cover about 12 cells at the hind-margin of the wing. A second transverse band 4 or 5 cells wide, under the pterostigma, but not quite reaching the hinder border of the wing. The fore wings have thus eight belts of colour altogether. Size a little smaller than *selysi*, postnodals 18-20	*O. octomaculata* Martin.
II. Wings with feeble pigmentation.	
c. The whole of the narrow area of the wing lying between the costal margin and the radius lightly tinged with greyish brown, the rest of the wing "smoky" (in adult male). Venation relatively denser than in *O. selysi*. Post-nodals 18-20. Hind wing 28·5 mm. in length	*O. wallacei* Kirby.

Selysi is recorded from Assam and Tonkin, *octomaculata* is known from a single male from Tonkin, described by Martin ('Mission Pavie, Zoologie, Liste des Névroptères de l'Indo-China,' sep., pp. 17–18).

I have seen examples of *wallacei* from Borneo and from the Malay Peninsula.

Thus the Synlestidæ are represented in Tropical Asia by three species of *Orolestes* and two of *Megalestes*.

PLATYCNEMIDÆ.

CALICNEMIS CHASENI, sp. n.

1 ♂ (holotype), Jor. Pahang, 4. vi. 22 (*F. Chasen*, Singapore Museum). Rather damaged.

Length of abdomen 26 mm. (circa), of hind wing 22 mm.

Head. Lower lip brownish yellow. Upper lip, genæ, and anteclypeus brownish red, the rest of the dorsal surfaces of the head black, with a red band across the frons at the level of the base of the antennæ. A small transverse post-ocular streak of yellow behind each eye.

Prothorax black above, lateral margins and ventral surfaces brownish yellow.

Meso-metathorax. Dorsal surface black, with a carmine-red stripe on either side of the middle line, pointed above and below. The black colour extends laterally as far as the first lateral suture, the rest of the sides and ventral surfaces yellow, with a black stripe along the upper half of the second lateral suture.

Abdomen almost entirely red. The first segment is yellowish with a square black mark on its dorsum Segments 3–7 rather carmine-red, the remainder more of a brown-red. Intersegmental sutures marked with very dark brown. On the ventral surface the colour is paler with a yellowish tinge.

Legs black, coxæ, trochanters, and anterior surface of femora brownish yellow.

Anal appendages (unfortunately, detatched from the abdomen) black, upper pair slightly longer than lower, rather lancet-shaped, slightly bent downwards; lower pair slender, curved inwards apically. 15–16 postnodal cross-nerves on fore wing.

The holotype is deposited in the British Museum.

This species is closely allied to *C. eximia* and to *C. miniata*, but smaller and rather slenderer than either. From *eximia* it differs in having the legs largely marked with black, whilst *miniata* is distinguished by black markings on the dorsum of the hinder segments of the abdomen. The occurrence of a true *Calicnemis* so far south is a surprise; there is, however, an unidentified specimen of the genus in the British Museum Collection from the N. Andaman Islands collected by Col. Bingham.

CŒNAGRIONIDÆ.

TEINOBASIS NIGRA, sp. n. (Campion MSS.). (Text-figs. 2 & 3.)

1 ♂ (holotype), Mt. Makiling, Luzon (16504, *C. F. Baker*).

Length of abdomen 36 mm., of hind wing 21·5 mm.

Head. Labrum whitish, upper lip, clypeus, and ridge on frons glossy black; upper surface of head including the occiput dull black, antennæ pale brown.

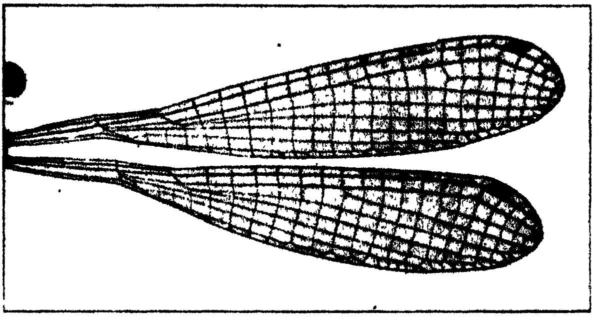
Prothorax blue-black, the posterior lobe rounded, almost vertical.

Meso-metathorax. Dorsum deep blue-black, as are the mesinfra-episternum and mesepimeron; metepisternum deep blue-black above the stigma and obscurely black below the stigma; metepimeron and ventral surfaces obscurely blue-black.

Legs yellowish; a blackish longitudinal line on external surface of each femur and tibia, and a narrow black ring at the apex of each tarsal joint.

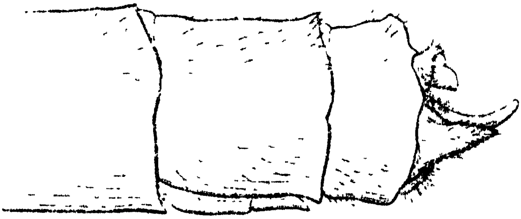
Abdomen very slender, somewhat dilated at segments 1 and 2 and 7–10; deep blue-black dorsally, with a pale ring at the base of 3–7; sides of 1–6 pale brown, 7–10 black. Ventral aspect coloured like the sides.

Text-figure 2.



Wings of holotype male *Teinobasis nigra.* (F. W. Campion photo.)

Text-figure 3.



Apex of abdomen of holotype male *Teinobasis nigra.*

Anal appendages **(text-fig. 3) blackish, the upper appendage on either side has its upper branch about one-half the length of the lower branch. This latter is gently curved upwards and is longer than the lower appendage, which is stout and conical. Both pairs shorter than segment 10.**

Wings **tinged with brown. Pterostigma covering one cell,**

rhomboidal, black, finely bordered with yellow. The anal crossing lies much nearer the level of the second antenodal than of the first. M_3 and *Rs* quite separate at their origin, though close together, the subnodus lying midway between them. 16 postnodals.

♀ (allotype), same data as for male.

Head. Labium whitish. Labrum brownish yellow, narrowly lined with black posteriorly. Clypeus bright brown, the junction with the frons lined with black. Genæ and anterior aspect of frons yellowish. Upper surface of head, including occiput, dull black. Antennæ pale brown.

Prothorax greenish brown, the posterior lobe rounded, almost vertical.

Meso-metathorax. Dorsum reddish brown; sides, below the humeral suture, greenish yellow; ventral surfaces yellow.

Legs yellowish; blackish markings as in male.

Abdomen very slender, somwhat dilated at segments 7–10. Segments 1–6 black dorsally, with fine whitish rings at the intersegmental sutures. On 7 the black of the dorsum recedes from the sides at the apex of the segment, giving place to reddish brown, which invades the venter and dorsum from the sides. Eighth segment with a mid-dorsal stripe of black, otherwise reddish brown. Segments 9–10 olive-green, dorsum of each mainly black.

Wings tinged with brown, pterostigma greenish brown, bordered with yellow. Otherwise as in male.

This species differs from its congeners in having M_3 and *Rs* separate at their origin, *Ac* nearer the level of the second antenodal than that of the first, and in having the lower branch of the upper anal appendage longer than the upper branch.

In colouring it resembles rather closely *kirbyi* Laidlaw from the Malay Peninsula (and ? Borneo), whilst its anal appendages are likewise similar to those of that species. It differs, however, entirely in venation.

Type ♂ in the British Museum.

[Since these notes went to press Dr. Ris has transferred the Sumatran species *Lestes udeana* Krüger to the genus *Orolestes*. It is apparently closely allied to *wallacei* and adds a fourth species to the genus. Ris, Zool. Meded. 's Rijks Mus. v. Nat. Hist. Leiden, x. Afl. 1927, pp. 11–15 (figs. 4, 5, 6).]

8. The Delacour Exploration of French Indo-China.—Mammals. II. On Mammals collected during the Winter of 1926–27. By Oldfield Thomas, F.R.S., F.Z.S.

[Received December 5, 1927: Read February 21, 1928.]

In a previous paper under this heading I gave an account of the fine collection of Mammals obtained by Messrs. Delacour and Willoughby Lowe in Tonkin and Burma during the winter of 1925-26, when no fewer than 72 species and subspecies were found in the area explored.

I now have the pleasure of giving a list of a second collection obtained by those two naturalists during the winter of 1926–27, in the same two countries, but for the most part at more southern localities than those previously explored. A considerable number of more southern forms, previously only known from Cambodia and Cochin China, are therefore included, while many of the northern Tonkin forms drop out.

During this trip the smaller terrestrial mammals had for various reasons to be somewhat neglected, so that little has been added to our knowledge of the Rodents, other than Squirrels, or of the Insectivores and Bats. But a particularly fine collection of Monkeys was made, among them being several remarkable species previously only known by single examples, such as *Hylobates concolor gabriellæ* from South Annam, and the northern *Pithecus francoisi* and *poliocephalus* described by the Paris naturalists and not previously represented in the British Museum. And there is a good series of the equally remarkable *Pygathrix nigripes*, only previously obtained for us by Dr. Vassal. The collection therefore adds very considerably to our knowledge of these various rare Monkeys, and by the liberality of M. Delacour causes an important increase in our material of them.

As on the previous occasion, the expedition was largely helped by the Percy Sladen and Godman Exploration Funds, and the Trustees of these are to be thanked for the valuable results that have accrued.

This second collection consists of about 300 specimens, belonging to 68 species and subspecies. In the previous paper 72 species are mentioned, and 35 in the still earlier paper on Mammals obtained by Mr. Stevens in Tonkin.

The most important localities worked this time by Messrs. Delacour and Lowe were:—Tam-Dao (3000′); Bac-kan (500′); Ngan-son (500′); and Langson (500′) in Tonkin; Thua-luu near Hué, Annam, and, most important of all, Djiring (3000′) in South Annam, where many of the most interesting species were obtained, representing forms described from still farther south, in Cochin China.

1. HYLOBATES CONCOLOR GABRIELLÆ Thos.

♂. 693. Djiring, S. Annam.

Precisely similar to the hitherto unique type of *gabriellæ*, and therefore of much interest in confirming the distinction of that form from *leucogenys*, on which some doubt has been thrown. We now see that *gabriellæ* is a genuine wild form, and not merely based either on an accidental variation or on an imperfectly-preserved skin.

In Mr. Pocock's recent paper on *Hylobates* *, *H. leucogenys*, and *gabriellæ* are both considered as subspecies of *H. concolor*, a conclusion which is supported by the essential identity in the skulls of all three. He also gives confirmatory evidence about the remarkable changes in colour that occur at different ages in *H. leucogenys* which were recorded by me, on M. Delacour's authority, in my previous paper.

2. PRESBYTISCUS AVUNCULUS Dollm.

♂. 425, 426 (young), 474, 506, 509, 522, 529, 544. ♀. 484, 508, 519, 523. Bac-kan, Tonkin, 500'.

A most valuable and interesting series, and one which shows that this fine monkey described by Dollman and hitherto only known from the type and its infant paratype, is a more remarkably-coloured animal than has been previously recognized.

I may first recall that Dollman's *Rhinopithecus avunculus* was made the basis of a new genus—*Presbytiscus*—by Pocock †, on account of the structure of its hands and feet, which are much slenderer and with longer digits than those of *Rhinopithecus*, a character quite confirmed by the present specimens.

Whereas in the type of *P. avunculus*, which came from Yen-bay, perhaps 100 miles from Bac-kan, the crown and nape are uniformly black, little or not lighter than the back, while the face and throat are a dull whitish, well-marked specimens of the present series show a much more striking coloration. The forehead and cheeks are a snowy white, then on the crown there is a transverse blackish band, rather over an inch in breadth, which runs outwards and backwards to the hinder edges of the ears. Succeeding this the whole of the nape is a fawn-grey, much paler than the deeply black back. Below, the whole of the neck, from side to side, is occupied by a prominent ochraceous patch, which varies however in its depth and extent. It is indeed scarcely perceptible in the type.

At first there seemed some doubt as to whether the Bac-kan monkey really was *avunculus*, so different did the extremes appear. A study of the whole series, however, shows such variation in the colour of the nape and its degree of contrast with the forehead and crown, and in the depth of the orange of the throat-patch, that I have now no doubt that the two should be considered as specifically identical with the type, which is a female, unusually dull coloured, dark naped, and whitish throated.

---

* P. Z. S. 1927, p. 719.

† Abstr. P. Z. S. 1924, p. 17.

A baby specimen has pale brown hands and whitish feet, these parts in the adult being deep black.

3. PYGATHRIX NIGRIPES M.-Edw.

♂. 621, 629, 692. ♀. 614, 622, 628. Djiring, 3500′.
♂. 623. ♀. 544 (babies). Djiring.
Three native skins, unsexed. Djiring.

A most acceptable addition to our small series of this fine monkey, of which we had previously received examples from Lang Bian and Bali, collected by Dr. Vassal.

The variation within the series in the extent of the black markings renders me somewhat dubious as to the subspecific distinction from *nigripes* of Mr. Kloss's *Presbytis nemæus moi*, of which one of Dr. Vassal's specimens is a topotype and to which all of our Annam examples are presumably referable. I admit that I have not had the opportunity of examining Saigon specimens representing true *nigripes*, but the resemblance of those we have to Milne-Edwards's figure is very close.

Nor, on the other hand, is there anything in the whole series available of this genus to support Mr. Kloss's reference to *nigripes* as only a subspecies of *nemæus*, the striking colour-differences being well marked in all, without any tendency to intergradation. No doubt the two are essentially very closely allied, but I should prefer to call them distinct species until some evidence of intergradation is brought forward. The comparative nearness of the localities, without intergradation, would seem to uphold the specific distinction of the two.

The baby specimens, Nos. 544 and 623, are of great interest, as the baby coloration of all the monkeys is very characteristic. In the youngest, No. 544 (♀), the general body-colour is whitish, above and below, a darker wash along the middle area of the back blackish. The crown and nape are covered with hairs, white basally and red at their tips, those on the triangle at the base of the tail, which is white in the adult, similarly white basally and red terminally, an ill-defined blackish transverse band just in front of it. Thighs whitish; knee region blackish; feet pale brownish. No. 623 (♂) has the crown more blackish, and its dark lumbar band is blacker.

4. PITHECUS POLIOCEPHALUS Trouess.

♂. 550. From the Hanoi Zoological Gardens.

Like *P. françoisi*, new to the British Museum, and consequently a very acceptable acquisition. Both these species were excellently figured by Trouessart in 1913 *.

---

* N. Arch. Mus. iv. pls. ii. & iii.

The type came from Kaï-chin, north eastern Tonkin.

The coloration is quite as figured by Trouessart except that there is rather less yellow on the throat, while the lumbar grey band is of rather greater extent. The great length and beautifully fine nature of the fur is a striking character of the species.

5. Pithecus germaini M.-Edw.

160. Cochin China. Delacour and Jabouille Coll.
218, 281. From the Zoological Gardens, Saigon.

6. Pithecus françoisi Pous.

♂. 543. Bac-kan, 500′.
♂. 581. ♀. 530. Langson, Tonkin, 500′.
♂. 211. From Saigon Zoological Gardens.

The type was obtained just across the Tonkin-Chinese frontier in Kwang-si. The species is new to the British Museum.

When describing the closely-allled *P. laotum*, I commented on the rock-haunting habits of these two monkeys, and this observation is confirmed by Mr. Lowe, who notes on one of the specimens "a rock-loving species."

7. Macaca mulatta Zimm.

♀. 449, 481, 507, 527, 550. Bac-kan, 500′.

Attention may be drawn to Messrs. Hinton and Wroughton's support of the name *mulatta* for the common Rhesus Macaque *.

8. Macaca fascicularis group.

14, 114, 260. From the Saigon Zoological Gardens.

I may take this opportunity of withdrawing the opinion I expressed in the previous paper as to F. Cuvier's *Macacus speciosus*, whose identification appeared to me to be too doubtful to be accepted. But I find that Mr. Pocock, whose knowledge of the living animals is so far superior to mine, had previously † identified it with the Burmese-Annam animals, which I called *arctoides*, and used the name *fuscata* for the Japanese monkey. On his authority, therefore, I am prepared to accept this view, and replace *arctoides* by *speciosa* for the Burmese species.

9. Pteropus vampyrus malaccensis K. And.

600. Near Hué, Annam.

10. Rousettus leschenaulti Desm.

One young. Bac-kan.

---

* J. Bomb. Soc. xxvii. p. 665 (1921).
† P. Z. S. 1925, p. 1497.

11. CYNOPTERUS SPHINX Vahl.

Two from Hué.

Similar to Tenasserim and Malay specimens, with very prominent ear-edge and white digits. Ears 22 mm.

The division between *sphinx* and *brachyotis* by the length of the ears is very unsatisfactory.

12. RHINOLOPUS AFFINIS Horsf.

Five from Langson.

13. HIPPOSIDEROS ARMIGER Hodgs.

Five from Djiring, S. Annam; one from Bac-kan.

Perhaps representing *H. a. debilis* K. And.

14. HIPPOSIDEROS BICOLOR Temm.

One from Bac-kan.

15. PIPISTRELLUS TRALATITIUS Horsf.

♂. 402, 410. 411. Tam-Dao, Tonkin, 3000.

In the two previous Tonkin papers I was content to record the specimens of Pipistrel obtained simply as *Pipistrellus* sp., but I have now been able to examine more closely all the Annam-Tonkin members of this interesting genus with a view to their better determination.

The species of *Pipistrellus* are largely distinguishable by the characters of their penis-bones, or bacula, which show very considerable diversity, and by the expert assistance of Mr. W. R. Sherrin in the preparation of these tiny bones I have been able to note the following characteristics of the Indo-Chinese species of this genus:—

A. Baculum with a double curvature.
  Baculum very long, about 10–12 mm. Skull 12·2 mm. *P. abramus* Temm.
B. Baculum approximately straight.
  a. Baculum very long, about 9–10 mm.
    Size larger. Forearm 38 mm. Skull 14·6 mm. . . . *P. raptor* Thos.
  b. Baculum of médium length—5–6 mm.
    Forearm 33 mm. Skull 13·5 mm. .... *P. tralatitius* Horsf.
  c. Baculum small—2·5–3 mm.
    Forearm 30 mm. Skull 12 mm. .... *P. coromandrus* Gr.

Specimens of *P. abramus* were obtained by M. Delacour at Hué in his first collection, while *P. raptor* has not been captured since the original specimens were received in 1904 from "Tonkin." Mr. Stevens's Pipistrels were referable to the species obtained by M. Delacour at Bac-kan. This would appear to be specifically referable to the Indian *P. coromandrus*, but the Further India specimens differ sufficiently to observe a special subspecific name, as follows:—

16. PIPISTRELLUS COROMANDRUS[*] TRAMATUS, subsp. n.

Ten specimens. Bac-kan, Tonkin.

[3 ♂, 4 ♀. Thai-Niên, Tonkin (*H. Stevens*).]

General characters as in S. Indian *P. coromandrus*, as identified by Wroughton, but the skull smaller and more lightly built, the muzzle lower, more slender, and the brain-case less broad behind.

Baculum small; that of the type 2·5 mm. in length, with a terminal fork.

Dimensions of the type:—

Forearm 29·5 mm.

Head and body 38 mm.; tail 28·5; ear 10·5; lower leg and hind-foot (c. u.) 16.

Skull: greatest length 11·8 mm.; condylo-basal length 11·4; basi-sinual length[†] 8·6; breadth of brain-case 6·1; mastoid breadth 6·6; maxillary tooth-row 4·1; front of p^1 to back of m^3 2·7.

Type. Adult male in spirit. B.M. No. 25.1.1.120. Original number 109. Collected 30 March, 1924, by Herbert Stevens. 20 specimens.

All the Tonkin and Annam specimens in the Stevens and Delacour-Lowe collections, as also one obtained by Mouhote in Cambodia, agree in the more delicate build of the skull as compared with true Indian *coromandrus*, but there does not seem to be any more tangible differential character, and I therefore provisionally recognize the present animal merely as a local subspecies.

17. SCOTOPHILUS KUHLI Leach.

Three from Bac-kan.

One specimen is of the large dark-coloured type, with yellow belly, similar to that which is usually found on the continent of India, while another is of the smaller kind usual in the Malay Peninsula.

18. TUPAIA BELANGERI TONQUINIA Thos.

Six from Bac-kan, one from Chora, Tonkin, and two from Thua-luu, Annam.

Being all from the northern part of the area treated of, these Tree-Shrews do not show any approach to the Nha-trang *T. concolor* Bonhote.

---

[*] I fail to see any reason why the word *coromandra*, used in that form by Gray, Wroughton, and others, should not be made to conform to the usual rule as to the termination of adjectival names.

[†] *Cf.* P. Z. S. 1908, p. 638.

19. **Dendrogale frenata** Gr.

♂. 598, 707. ♀. 703, 704. An-Bink, Cochin China.

No. 598 has all the buffy elements of its colour intensified, the belly being strongly ochraceous, while the lower light facial line is even ferruginous. But the other specimens are as usual.

20. **Felis tigris** L.

Native skin without history.

21. **Felis pardus** L.

Native skin—melanoid—no history.

22. **Felis viverrina** Benn.

Native skin without history.

23. **Felis marmorata** Mart.

♂. 552. Bac-kan, Tonkin.

24. **Felis bengalensis** Kerr.

Eleven from Bac-kan, one from Ngan-son, Tonkin, and one from Hué, Annam.

25. **Herpestes urva** Hodgs.

Ten from Bac-kan (500′) and six from Langson.

26. **Herpestes exilis** Gerv.

Native skin.

27. **Viverra zibetha** L.

Two males and three females from Bac-kan, Tonkin.
♀. Phurieng, N. Cochin China (P. 1).

28. **Viverricula malaccensis** Gm.

♂. 571, 572, 573, 574. Langson, Tonkin.
♀. P. 2, P. 3. Phurieng, N. Cochin China.

29. **Pardictis pardicolor** Hodgs.

♂. 485. ♀. 512, 528. Bac-kan, Tonkin, and one native skin from near Hanoi, Tonkin.

30. **Paradoxurus birmanicus** Wrought.

♂. 557. Hué, Annam.

31. **Paguma larvata yunalis** Thos.

♀. 446. Bac-kan, Tonkin, 500′.

32. ARCTICTIS BINTURONG Raff.

One skin from Tonkin.

33. CHROTOGALE OWSTONI Thos.

491. Ngan-son, Tonkin, and four native skins without exact locality.

In reference to my previous note on *Chrotogale*, a protest has reached me from America as to the opinions I have credited to the advocates of the trituberculer theory, and I am willing to confess that in supposing them to believe the Cat's dentition to be primitive I have maligned them. In fact, I am assured by Mr. Miller that the trituberculariats would say, as I do, that the *Chrotogale* dentition is primitive, and that of the Cat specialized. And so for this I must apologize, but, all the more, my objection to Mr. Le Gros Clark's statement that, because it is more simple, the dentition of *Ptilocercus* is more primitive than that of *Tupaia* would seem to have been needed.

34. CYNOGALE BENNETTII Gray.

477 (immature). Bac-kan, Tonkin, 500 ft.

35. CUON RUTILANS Müll.

♀. 551. Bac-kan, Tonkin.

One native skin.

36. VULPES sp.

♀. 570. Langson, Tonkin.

37. NYCTEREUTES PROCYONOIDES Gray.

♂. 569. ♀. 568. Langson, Tonkin, 500′.

38. HELARCTOS MALAYANUS Raff.

♂. 553 (young). Hué, Annam.

39. MELOGALE PIERREI Bonh.

♂. 678. Djiring, S. Annam.

This specimen is of the usual grey colour, as found in *M. personata*, and the reddish tone of Pierre's specimens is probably due to bleaching. Whether *pierrei* is really different from *personata* remains to be seen. The type-locality of *pierrei* is Saigon.

40. MELOGALE PERSONATA LAOTUM Thos.

♂. 555. Hué, Annam.

41. LUTRA SUMATRANA Gray.

179, 199. Annam (*Delacour & Jabouille*). (Young.)

Recorded from Siam by Gyldenstolpe. A subadult male, skin and skull, from Long-Xuyen, Cochin China, obtained by Capt. E. Dorr in 1883, was included in the collection of mammals presented to the British Museum by M. Fernand Lataste in 1919.

I fail to see any sufficent reason for Pohle's resuscitation of Günther's *Lutra lovii* as distinct from *L. sumatrana*, and I should also doubt the validity of the former's *L. brunnea*, from Pontianak.

42. HYLOPETES ALBONIGER Hodgs.

♀. 613. Djiring, S. Annam.

43. HYLOPETES SPADICEUS Bly.

♂. 661, 662. Djiring, S. Annam.

44. RATUFA GIGANTEA McCl.

Five from Tam-Dao, Tonkin.

45. RATUFA BICOLOR SMITHII Rob. & Kl.

♂. 624, 615. ♀. 635. Djiring, S. Annam, 500′.

A well-marked subspecies, discovered by Mr. Boden Kloss on the Lang-bian Peaks, S. Annam; the type presented to the National Museum by Messrs. Robinson and Kloss.

46. CALLOSCIURUS CASTANEOVENTRIS CASTANEOVENTRIS Gray.

Seven from Tam-Dao, one from Chora, eight from Bac-kan, one from Langson, and three from Ngan-son.

All therefore from Tonkin, this species apparently not passing south into Assam.

47. CALLOSCIURUS FLAVIMANUS FLAVIMANUS Geoff.

♂. 593, 594. Thua-luu, Annam.

48. CALLOSCIURUS LEUCOPUS Gray.

Twenty-one skins and one in spirit. Djiring, S. Annam.
Four from An-binh.

For squirrels all from one locality, specimens from Djiring are unusually variable, mainly in the degree to which the general colour is clear grey or suffused with buffy, the legs are or are not buffy, and the whole belly surface is or is not washed with buffy.

In view of this variability, I am in doubt as to the validity of *C. leucopus vassali* Bonh. from Nha-trang, slightly to the north of Djiring. The three original specimens of it are all rather more sombrely coloured than in other examples of *leucopus*, and there is little trace of the light hip-patch generally present in that animal.

49. DREMOMYS RUFIGENIS Blanf.

Eight from Tam-Dao, three from Bac-kan, two from Thua-luu, one from Djiring.

Again, as with *Callosciurus leucopus* "*vassali*," we find a special dark form of *Dremomys rufigenis* (*D. r. fuscus*), described by Bonhote on a specimen from near Nha-trang, and the same problem crops up as with the *Callosciurus*. This is as to whether there is really a special faunal area near Nha-trang where the animals tend to be more saturate, or whether some method of preparation of the skins may not have affected the colour in each case.

It is hoped that fresh modern skins of these and other species will be obtained from the Vassal region, so that this question may be settled.

50. MENETES BERDMOREI subsp.

♂. 697. An-Binh, Cochin China.

Not determinable subspecifically at present.

51. TAMIOPS MARITIMUS Bonh.

Twenty-five specimens from Bac-kan and Tam-Dao, Tonkin, and Djiring, S. Annam.

Using as before the interruption of the subocular light stripe from that of the flanks as a specific character, I would provisionally refer these specimens from N. Annam and Tonkin to the *maritimus* of S. China, forms described from Formosa and Hainan being also very doubtfully separable. Those from Tam-Dao, Bac-kan, and other parts of Tonkin are dull coloured, closely similar to Fokien and other Chinese specimens and mainly separable from *macclellandi* by the interruption of the lateral stripe. A more showy animal, distinguished by the light lateral stripe being on the average much more strongly marked, is represented by the series from Djiring, unquestionably referable to Robinson and Kloss's *moi*, of which the type, now B.M. 26.11.17.7, from Lang-bian Peaks, S. Annam, agrees closely with them. But they are again so like Bonhote's *monticolus* that I fail to find any character by which they can be readily distinguished. This is a more or less saturate form, while Robinson and Kloss's *laotum* from the Mekong farther to the north is a "siccate" race, such as one would expect to find in an arid area. Though averaging paler it is indeed not unlike typical *manipurensis*, from which again it is separated by the interruption of the lateral light lines and the suffusion with rufous of the darker dorsal stripes. The specimens from Xieng Khouang in the previous collection prove to be referable to this race, of which the type has also now been presented to the British Museum, B.M. No. 26.11.17.6.

What the relation is to each other of the dull-coloured *maritimus* and *moi* I cannot at present understand. All the S. Annam specimens are "*moi*" and all the Tonkin ones *maritimus*, but in China the two corresponding forms are found some in our locality and some in another, without any evident reason for their distribution. Bonhote thought it to be a question of altitude, but the material available is not at present sufficient either to establish or confute his views.

52. TAMIOPS RODOLPHEI M.-Edw.

Eight from Djiring, Tonkin, four from An-Binh, Cochin China.

53. TAMIOPS INCONSTANS Thos.

Three specimens from Ba-Bé, Tonkin.

54. RATTUS EDWARDSI Thos.

♀. 502. Bac-kan, Tonkin.

55. RATTUS BOWERSI J. And.

♂. 514. Bac-kan, Tonkin.

56-58. RATTUS spp.

Fifteen specimens, apparently belonging to three species.

59. MUS DUBIUS Hodgs.

One specimen from Djiring and one from Ngan-son, Tonkin.

60. RHIZOMYS SENEX, Thos.

Ten specimens from Bac-kan, one from Langson, seven from Ngan-son, Tonkin.

61. ACANTHION sp.

♂. 427. Bac-kan, Tonkin.
♂. 554. Hué, Annam.

62. LEPUS VASSALI Thos.

♂. 646. ♀. 638. Djiring, S. Annam.
♀. 709. An-Binh, Cochin China.

63. SUS CRISTATUS Wagn.

♂. 692. ♀. 604. Djiring, S. Annam.

64. TRAGULUS KANCHIL PIERREI Bonh.

♂. 300. From Zoological Gardens, Saigon.
♀. 586. Thua-Luu, Annam.

65. Capricornis sumatrensis Shaw.

♂. 690. Vinh, Annam.
♀. 575. Langson.

66. Rusa sp.

♂. 681 (young). ♀. 684 (young). Djiring, S. Annam.

67. Cervulus muntjac Zimm.

♂. 473. ♀. 423, 422, 472. Bac-kan, Tonkin.
♀. 605. Djiring, S. Annam.

68. Phatages crassicaudata Geoff.

♂. 521. Bac-kan, Tonkin.

9. New Chrysomelid Beetles from India. With a Note on the Scales of Coleoptera. By S. Maulik, F.Z.S.

[Received December 9, 1927 : Read February 21, 1928.]

(Text-figures 1–5.)

CONTENTS.

Page
Description of *Squamispa*, gen. n. 151
Structure of Scales of *Squamispa* 152
General Considerations on Coleopterous Scales.................. 153
Affinity of the Genus *Squamispa* 153
Description of *Squamispa fasciata*, sp. n... 154
Description of *Squamispa ballapurana*, sp. n. 155
Description of *Agonia chlorina*, sp. n. 157
Note on the Genus *Wallaceana*, nom. n. 159
Note on *Monochirus capensis* Maulik and *Phidodonta chirinda* Maulik 159
Description of the Genus *Throscoryssa*, gen. n. 159
Description of *Throscoryssa citri*, sp. n. 160

The present paper is based on the material in the collection of the British Museum (Natural History). The microscopic slides prepared for the present study are in the same museum. I am indebted to Mr. A. J. E. Terzi for the drawings.

Subfamily HISPINÆ.

SQUAMISPA, gen. n.

Body very narrowly elongate; elytra narrowed at the base and much more so towards the apex, so that the greatest width is just behind the middle. The apex of the elytra is not produced to a sharp point. Prothorax much longer than broad, with the sides margined. Head with the upper side somewhat raised, with a channel along the middle, and not at all produced between the antennæ. The latter are eleven-segmented. The whole body, including the head, antennæ, thorax, elytra, underside, femora, tibiæ, and tarsi is covered with whitish semi-erect scales. The distribution of the scales on the body varies in the present new genus. On the upper side the discal area of the elytra is sparsely covered; on the sides, and especially on the apical area, they are more densely placed; on the underside and the legs the distribution is uniform. On the five basal segments of the antennæ the scales are distributed as on the head, but on the apical six segments they are scarce where more bristly hairs occur. Elytra regularly punctate-striate, without a scutellar row of punctures. Prosternal process narrow between the coxæ and widely expanded behind, almost into a circular shape. Legs short and stumpy; tibiæ very short, almost equal to the tarsi in length; claws strongly developed, wide apart, pointing sideways. To this condition of the claws the term "divaricate" has sometimes been given in the group Longicornia, in which it is more common.

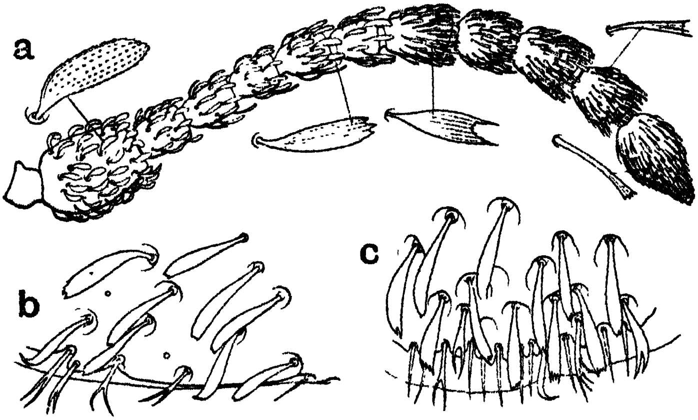
GENOTYPE, *Squamispa fasciata* Maulik, gen. n. et sp. n.

Range. South India.

Structure of Scales of Squamispa. (Text-fig. 1.)

The scales are deeply rooted and are not easily removed from their position. Each scale arises from a pore, and stands separate from its neighbours, somewhat bent. When it rises from the puncture of the elytra, its point of origin is not at the centre of the puncture. A scale is white, fairly long, narrow at its base, gradually broadening and somewhat narrowing towards the apex. Its surface is studded with extremely minute spinules; this can be seen when a scale in the preparation is in a bent position so that its surface appears convex. When a scale is laid flat, its surface seems to be longitudinally ridged, presumably, according as these minute spinules are arranged. Boiling in caustic potash has apparently very little action on the scales. They stain satisfactorily when kept in Ziehl's Carbolic Fuchsin for about twelve hours.

Text-figure 1.



A. Right antenna of *Squamispa fasciata* Maulik, showing distribution of scales.
B. Scales on last dorsal abdominal sclerite.
C. Scales on last ventral abdominal sclerite.

General Considerations on Coleopterous Scales.

Through the courtesy of Dr. G. A. K. Marshall, C.M.G., F.R.S., I have been able to examine two species of the family Curculionidæ which are pre-eminently scaly Coleoptera. These are *Rhigus schüppeli* Germ. and *Germariella pudens* Boh. From a study of the scales of these two species and that of *Squamispa* Maulik the following general ideas can be formulated:—

(1) The scales are modified hairs. The latter term is used in the sense in which it is generally applied to the clothing of insects.

(2) Between the two extreme forms, namely the elongate hair and the more or less rounded flattened scale, there are many varieties of transitional forms. Although owing to their particular arrangement and order these forms may have received various names for classificatory purposes, morphologically they are homologous.

(3) The upper surface of a scale has always a structure which varies considerably, the underside being generally plane.

(4) Scales of different forms may occur either together on the same part or separately on different parts of one and the same insect.

(5) A scale is attached to the surface at a little pore.

(6) The strength of attachment varies; the more elongate forms are strongly attached and are not removed easily from their point of attachment, while the scales of the more rounded and flat forms are not deeply rooted and can be more easily removed.

(7) The various colours of the scales are due partly to the surface structure and partly to pigment, and often due to both factors.

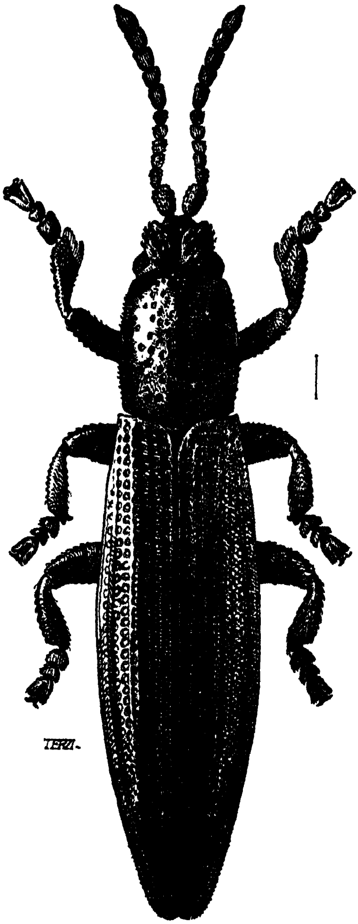
(8) Probably the modification of the hair into a true scale is accompanied by a corresponding chemical change.

In a paper by George Dimmock, entitled "The Scales of Coleoptera," published in 'Psyche,' 1883, pp. 3–11, 23–27, 43–47, 63–71, there are many references to previous papers relating to this subject. Although much attention has been paid to the scales of the Lepidoptera, those of the Coleoptera have not been thoroughly studied. More research, particularly from the chemical standpoint, will reveal many new facts.

Affinity of the Genus Squamispa.

The present new genus *Squamispa* is related to *Eurispa* Baly by the form of the body, but differs from it in that in *Squamispa* the apices of the elytra are not produced into sharp spines as in *Eurispa*. In his description of the genus, Baly does not say anything about the occurrence of scales on the head and prothorax of *Eurispa vittata*, the genotype, which I have examined in the collection of the British Museum. In view of the fact that *Squamispa* is completely covered with similar scales, their presence at least on certain parts of the body in *Eurispa* affords another point of affinity between the two genera. *Eurispa* spreads from Tasmania, South and North Australia to New Guinea, while *Squamispa* has so far only been found in South India. It is quite possible that such scaly members of the Hispinæ would occur in the Indo-Malayan regions.

Text-figure 2.



Squamispa fasciata Maulik. (× 18.)

SQUAMISPA FASCIATA, sp. n. (Text-fig. 2.)

Colour of head, eyes, prothorax, first segment of antennæ and underside black; the ground-colour of elytra and the remaining ten segments of antennæ pitch-brown; along the suture and on each side covering an area to the fourth interstice, counting from the suture, there is a darker stripe, and an ill-defined area on each side, and especially towards the apex, is similarly darker-coloured. Scutellum black.

Head as in the genus; antennæ with the first segment thick, cylindrical, second and third about equal, fourth, fifth, and sixth equal to each other, from the seventh to the eleventh the segments are larger and together form a sort of elongate club. *Prothorax* much longer than broad, sides parallel, front margin gently arched. The upper surface is generally shagreened, and, in addition, there are some large deeply impressed punctures which are not placed very close together, though comparatively more so on the discal and lateral than on the anterior or posterior areas. *Scutellum* very small, triangular. *Elytra* as broad at the base as the prothorax. On each elytron there are eight longitudinal series of deeply impressed fairly large punctures; a shorter ninth series commencing from the middle is visible when seen from the ventral aspect, because the interstice between the eighth and ninth rows is strongly costate. All the rows converge on the apical area. The interstices between the rows are fairly broad, raised, and with their surface rough. Along the fourth and fifth interstices, and particularly where they terminate, the elytral surface is depressed. *Underside* roughly punctate; the abdomen is deeply sunk in the cavity of the elytra, and the divisional lines between the last three abdominal segments are deeply impressed. On each side at the base of the abdomen is a depression probably for the reception of the hind leg, which in repose is held tightly pressed against the body. The front tibiæ are rather shorter than the front tarsi and have on the underside of the apex a bunch of stiff brownish bristles. The first segment of the front tarsi is larger than the corresponding segments of the other tarsi. The underside is more densely covered with scales than the upper side. Other structures as in the genus.

	mm.
Length from the apex of head to apex of elytra ...	6
Greatest width	1¼
Length of antenna	1¾
Length of pronotum	1¼

SOUTH INDIA: Mysore, Chikkaballapura (*T. V. Campbell*). Ex. coll. E. A. Butler.

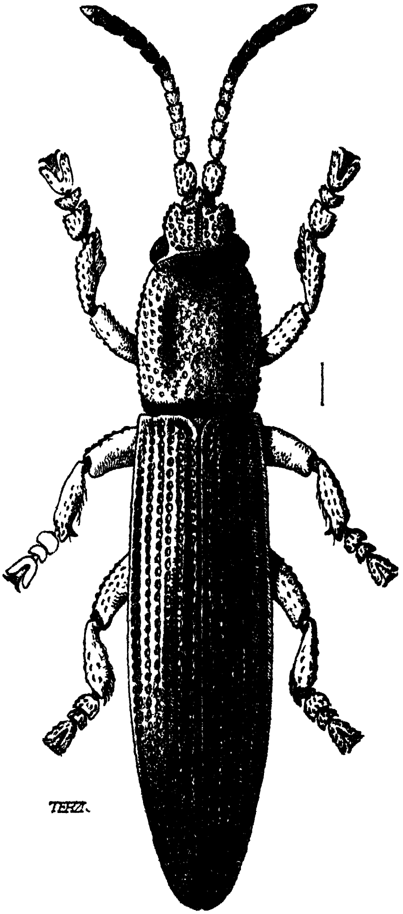
Type in the British Museum.

Described from one example.

SQUAMISPA BALLAPURANA, sp. n. (Text-fig. 3.)

Colour of elytra pitch-brown, with the lateral margins much lighter, almost yellowish; pronotum, head, and antennæ reddish brown; the anterior and posterior margins of pronotum and two ill-defined areas, one on each side of the middle line, black; eyes black; five apical segments of antennæ somewhat darker than the six basal segments; scutellum black; underside lighter than the upper side, with the lateral margins of the abdominal sternites blackish; some portion of the posterior femora and points of articulation of all joints pitch-brown. The whole body is subnitid, although the elytra appear at certain angles to be somewhat more shining.

Text-figure 3.



Squamispa ballapurana Maulik. (× 18.)

Head characters as stated in the generic description. Antennæ with the first segment cylindrical and large; the second is thicker than third, which in some aspects appears to be slightly longer than second; fourth, fifth, and sixth about equal to each other, each being slightly shorter than each of the preceding segments; from the seventh to eleventh the segments are thicker and somewhat longer, forming a sort of elongate club. *Prothorax* much longer than broad, cylindrical with the sides margined; front margin very gently arched, hind margin almost straight; upper surface covered with a mixture of comparatively finer and coarser punctures. *Scutellum* minute, triangular. *Elytra* as broad at base as the prothorax. On each elytron there are eight longitudinal series of deeply impressed and fairly large punctures; commencing from the middle along the extreme margin there is an additional shorter series. On the extreme apical area the series of punctures converge. The intervals between the rows appear to be more or less flattened and somewhat raised, the alternate ones much more so. *Underside*: from the mesothorax to the apex of the abdomen the body is deeply imbedded in the cavity of the elytra. The divisional lines between the last three visible segments are deeply impressed. Tibiæ shorter than tarsi in all the legs. In the front tarsi the first segment is much broader than the corresponding segment of the other tarsi; this is probably a secondary sexual character of the male, according to analogy of other genera in the Hispinæ. The bilobed segment of all the tarsi is deeply divided, the claw segment fitting suitably in the cleft. Claws as stated under the genus.

	mm.
Length from the apex of the head to the end of the elytra	5¼
Greatest width just behind the middle of the elytra	1¼
Length of pronotum	1¼
Length of antennæ .... about	2

South India: Mysore, Chikkaballapura (*T. V. Campbell*). Ex. coll. E. A. Butler.

Type in the British Museum.

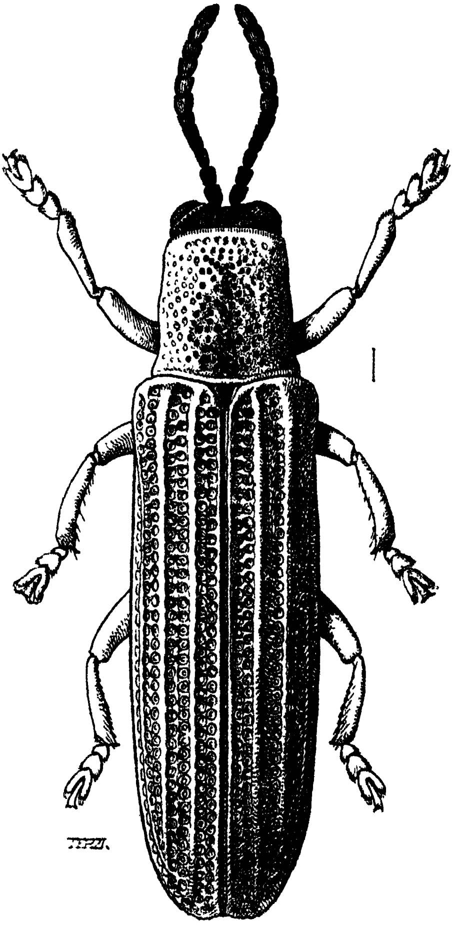
Described from one example.

Agonia chlorina, sp. n. (Text-fig. 4.)

Body very narrow, elongate, parallel-sided, with the apex rounded. Upper side and legs yellow, with the suture blackish; head, scutellum, and underside deep black; antennæ brownish, with four or five basal segments darker brown; some of the punctures have black centres; in one example an ill-defined short longitudinal stripe along the middle of the pronotum black.

Head finely shagreened, and with a few scattered punctures on the interocular area. Antennæ hardly reaching the base of the pronotum; the two basal segments cylindrical, thicker than the third, and almost equal to each other in length; third and fourth similar in thickness, but the third is slightly longer than fourth; from the fifth the segments begin to become thicker, so that the seven apical segments form an elongate club; fifth smaller than sixth; the remaining segments about equal except the last, which is somewhat longer and pointed; the last six segments are hairy. *Prothorax* subnitid, cylindrical, much longer than broad, parallel-sided, posterior lateral angles each with a pore bearing a seta, the front and hind margins almost straight; upper side somewhat convex in the middle and sloping at the sides, closely covered with deep punctures, a transverse row along

Text-figure 4.



Agonia chlorina Maulik. (× 24.)

the front margin; the punctures on the central area with their centres black. *Scutellum* rectangular, smooth, shining, and impunctate. *Elytra* subnitid, slightly broader at the base than the prothorax; punctate-striate, each elytron having four pairs of longitudinal series of deep punctures and three costæ; a scutellar row absent. The punctures on the discal area generally have black centres. *Underside* not hairy, shining, seen under a high power shagreened; metathorax sparsely covered in the middle with small punctures and the sides with coarser punctures; on each abdominal sternite is a transverse row of fine punctures across the middle, and on the sides there are some coarser punctures; on the last but one visible sternite the punctures are confusedly distributed on the surface. The middle tibiæ are shorter than others, somewhat curved, and with a spine at the apex.

Length 4 mm.; breadth 1¼ mm.

Length of second specimen 3 mm. and breadth 1 mm.

SOUTH INDIA: Nilgiri Hills (*T. V. Campbell*). Ex coll. E. A. Butler.

Type in the British Museum.

Described from two examples.

WALLACEANA, nom. n.

In the year 1858 Baly published in the 'Catalogue of Hispidæ' (British Museum publication) the name *Wallacea* for a genus of Coleoptera. In the same year Doleschall used the same name for a genus of Diptera which was published in the Batavian journal, Natuurkundig Tijdschrift v. Ned.-Indië, (4) xvii. p. 82. Although I have tried to ascertain definitely the exact dates of publication in both cases from all possible sources, I have not succeeded. But it seems that Doleschall's paper may have appeared a few months earlier than Baly's book. I therefore change the name of the Coleopterous genus into *Wallaceana*. The species that have hitherto been included in *Wallacea* should now fall under the genus *Wallaceana*, the genotype being *Wallacea bowringi* Baly (Java), which is in the British Museum.

Note on *Monochirus capensis* Maulik and *Phidodonta chirinda* Maulik.

Monochirus capensis Maulik and *Phidodonta chirinda* Maulik (Ann. & Mag. Nat. Hist. 1919, p. 407) are identical with *Monochirus capensis* Maulik and *Phidodonta chirinda* Maulik (Ann. & Mag. Nat. Hist. 1922, p. 569).

Subfamily HALTICINÆ.

THROSCORYSSA, gen. n.

Body ovate, convex. Head with the vertex not strongly convex, the interocular space with two deeply impressed channels,

each obliquely directed from the apex of the eye towards the centre; frontal tubercles absent, although the interantennal space is not quite flat. Antennæ extending to a little distance beyond the humerus, six apical segments thickened. Elytra very regularly punctate-striate with a long scutellar row. Wings present. Anterior coxal cavities closed behind. Intercoxal process of the prosternum punctate. Each front tibia with one spine at the apex; middle and hind tibiæ each with two spines at the apex, one of which is larger than the other. Posterior tibiæ not channelled on the upper surface. First segment of the posterior tarsi not very long. Claws simple.

GENOTYPE, *Throscoryssa citri* Maulik, gen. n. et sp. n.

Range. India.

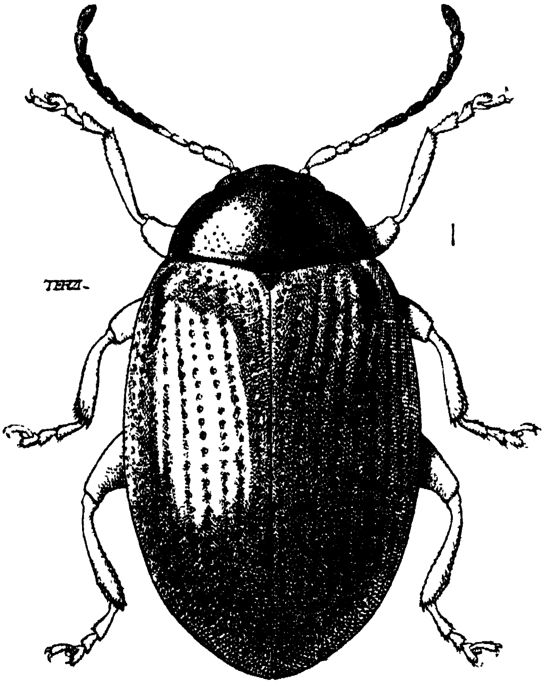
According to the arrangement proposed in my book on Halticinæ in the 'Fauna of British India' series (Taylor & Francis, London, 1926), this new genus should fall under Section III, Subsection III. (see p. 174), which is characterised as follows: "Pronotum and elytra not pubescent (except in *Ophrida hirsuta*); claw-segment of hind tarsi not greatly dilated; front coxal cavities closed or almost closed behind." In working with the table given on p. 174 the present new genus would come near *Kamala* Maulik. Although it bears a superficial resemblance, it is not really related to it because *Kamala* Maulik is apterous, whereas the present new genus has the genotype with fully developed wings.

THROSCORYSSA CITRI, sp. n. (Text-fig. 5.)

Body ovate. Colour shining brown with head and prothorax shining black; the basal segments of antennæ brownish, fourth segment partly brownish and partly piceous, remaining six segments piceous. Scutellum partly brown and blackish.

Head with the vertex smooth, finely and sparsely punctate; other characters as in the generic description. Length of antennæ as stated in the generic diagnosis; first segment large, club-shaped: second thicker but shorter than third, the latter slightly longer than fourth; from the fifth the segments have become larger, thicker, and more hairy; the last slightly longer and bluntly pointed. *Prothorax* much broader than long, slightly narrowed anteriorly, posterior margin somewhat produced into a broad lobe in the middle; sides gently rounded, margins slightly reflexed and with a row of punctures along each margin; each of the anterior lateral angles with a pore bearing a fine seta; upper surface convex, sloping down at each side, fairly closely and finely punctate, although the punctures are coarser than those on the vertex of the head; the punctures on the pronotum are not uniformly distributed, there being impunctate areas. *Scutellum* sharply triangular, smooth, and impunctate. *Elytra* almost as broad at base as the prothorax, then slightly widened behind and gently narrowing again towards the apex. Regularly punctate-striate, each elytron having eleven longitudinal rows of punctures, including a long scutellar and an extreme marginal one; the rows converge on the apical area. Seen under a high power, the intervals between the rows do not appear to be quite flat, and they bear very minute scattered punctures; the intervals are of equal width except the last along the margin, which is wider. *Underside* smooth, shining, not hairy, very finely sparsely punctate. Other characters as under the genus.

Text-figure 5.



Throscoryssa citri Maulik. (× 24.)

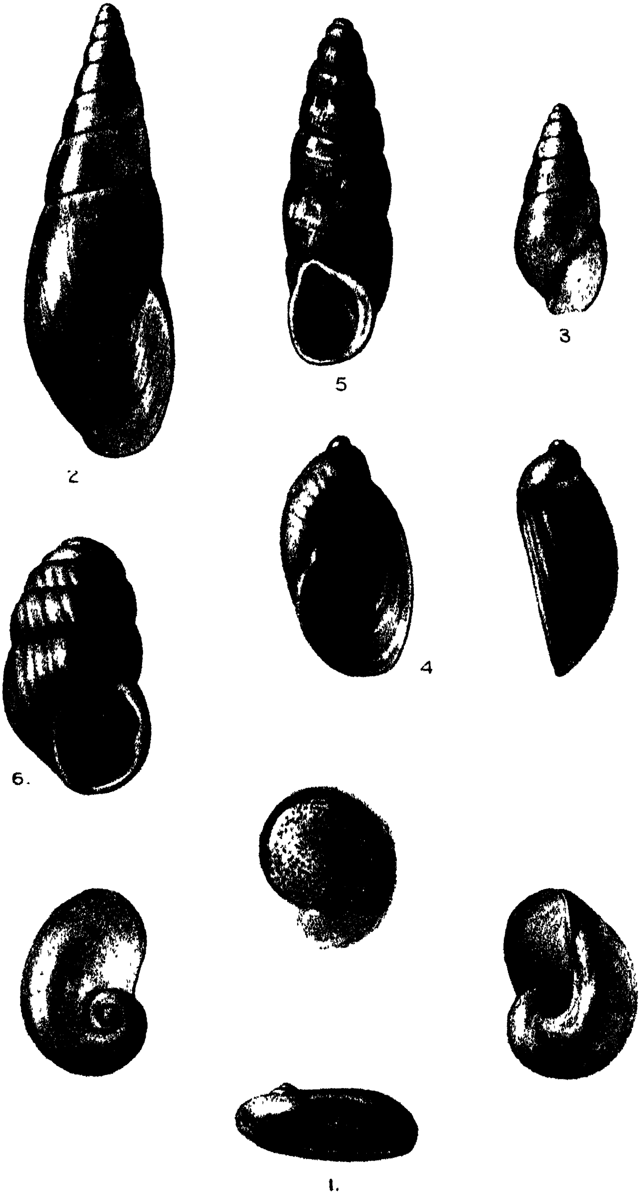
Length 3 mm.; breadth 2 mm.

Assam: Shillong, 20 iii. 1926 (*C. P. Clauson*). On orange trees. Larvæ, leaf-miners.

Type in the British Museum.

Described from twenty-one examples.

P Z S 1928, CONNOLLY, Pl. I



John Bale, Sons & Danielsson Ltd

MOLLUSCA FROM SOUTHERN ABYSSINIA.

10. On a Collection of Land and Freshwater Mollusca from Southern Abyssinia. By M. CONNOLLY*.

[Received December 22, 1927: Read March 6, 1928.]

(Plate I.†; Text-figures 1–4.)

CONTENTS.

	Page
1. Introduction	163
2. Systematic, including descriptions of six new species	164
3. A Survey of the Molluscan Fauna of Abyssinia	178
4. Bibliography	183

1. Introduction.

It is particularly difficult for a worker in England to study the fauna now under notice, since, almost incredible as it may appear, there has been only one short paper written on the subject ‡ in the English language, and authentic examples of the large number of species which have been described from Abyssinia are almost non-existent on this side of the English Channel.

True, the Continental authors who have dealt with them have, as a rule, taken infinite pains to make their descriptions as lucid as possible; but it is never satisfactory to attempt to identify a shell from literature alone, and many supposed new species have been based on short series in bad condition, to examine which would necessitate a journey over nearly half Europe.

The present collection, which was made by Dr. Hugh Scott and Mr. J. Omer-Cooper in 1926, covers roughly a district of about 120 square miles, situate between 7° and 9° N. Lat. and 38° and 39° E. Long., and the Ragazzi Collection, elaborately treated by Pollonera ‡, was partly made in the same area, so that it has been a simple matter to apply many of his names to the species hereafter mentioned; but I do not venture into the questions of synonymy, which will inevitably arise if anything like a representative collection from Abyssinia can be assembled.

As many of the localities to be recorded are found on few, if any, maps, I give their exact position, as far as possible, but it must only be accepted as narrowly approximate. The whole collection has been kindly presented to the British Museum.

---

* Communicated by G. C. ROBSON, M.A., F.Z.S.

† For explanation of the Plates see p. 184.

‡ See Bibliography, p. 183.

2. Systematic, including descriptions of six new species.

GASTROPODA.

Family STREPTAXIDÆ.

Subfamily *PTYCHOTREMATINÆ*.

Genus PTYCHOTREMA Mörch, 1852.

PTYCHOTREMA DENTICULATUM (Morel.).

1872. *Ennea denticulata* Morel., Ann. Mus. Genova, iii. p. 202, pl. ix. fig. 10.

Hab. Zukwala, 9000 ft., 8° 45′ N. Lat. and 38° 80′ E. Long.; Jem Jem Forest, 8000 ft., 9° N. Lat. and 38° E. Long. (*Omer-Cooper*).

Two examples from Zukwala are 6·9 and 6·0 mm. in length, while the Jem Jem shells measure 5·0 and 4·5 respectively.

Var. ex forma NANA nov.

Hab. Jem Jem Forest (*Omer-Cooper*).

An almost exact miniature of the foregoing, but measuring only 3·1 × 1·2 mm. in length and breadth; the tubercle on the outer lip is comparatively stronger, and it is possible that further material may prove this to be a distinct species.

Genus GULELLA Pfr., 1856.

GULELLA SIMPLICIMA (Prest.).

Hab. Zukwala; Jem Jem Forest (*Omer-Cooper*).

Described from Mt. Kenya, it is rather surprising to find this species so far afield, but the Kenyan and Abyssinian examples are quite inseparable. The protoconch (two whorls) shows well-marked, continuous, microscopic spiral engraving, while the second whorl is also sculptured with close, fine, transverse striæ.

Family ZONITIDÆ.

Subfamily *VITRININÆ*.

Genus VITRINA Drap., 1801.

VITRINA BIANCHII Pollon.

1888. *Vitrina bianchii* Pollon., Boll. Mus. Torino, iii. no. 37, p. 1; id., Bull. Soc. Mal. Ital. xiii. p. 57, pl. ii. figs. 1–3, 17.

Hab. Zukwala (*Scott & Omer-Cooper*).

Both shell and animal agree with Pollonera's figures.

VITRINA MODESTA Pollon.

1898. *Vitrina modesta* Pollon., Boll. Mus. Torino, xiii. no 313, p. 3, pl. i. figs. 10–12.

Hab. Jem Jem Forest (*Omer-Cooper*).

The protoconch in the present series is very faintly, somewhat irregularly, spirally micro-punctate, and has close regular lines of short transverse scratches, the remaining whorls being microscopically malleate; it is imperforate at all stages of growth, thereby differing from *V. helicoidea* Jick., which appears to be a higher, more globose form. Pollonera makes no mention of microscopic apical sculpture in his description of *modesta*, but in other respects the Jem Jem shells seem to agree with his species, which was described from the Plain of Chereth.

VITRINA GROSSEPUNCTATA, sp. n. (Pl. I. fig. 1.)

Shell of fair size, depressed globose, imperforate, thin, smooth, glossy, transparent, corneous, pale yellow-olivaceous. Spire depressed, apex prominently mammillate. Whorls 3¼, convex, very rapidly increasing; protoconch (1¼ whorl) much exserted, closely studded which coarse micro-punctate dots, which are so thick together that they hardly form any radial or spiral pattern, and which continue more finely in an irregular legion, gradually becoming weaker and fainter, until on the beginning of the last whorl they are scarcely visible, and soon practically disappear; the whole of the base is faintly micro-punctate in close, wavy, dotted spiral lines, the dots being so close together as almost to appear to form continuous lines; suture simple, shallow. Aperture subovate; peristome simple, acute, outer lip curved upward and forward, then descending and receding to the base; columella weak, slightly adnately thickened.

Diam. maj. 11·1, min. 8·2; alt. 5·0; apert. alt. 4·5, lat. 7·3 mm.

Hab. Jem Jem Forest (type); Addis Abeba, 8100 ft. (*Omer-Cooper*).

From its prominent apex, I would have expected this to be *mamillata* Mts., but Dr. Thiele kindly informs me that in that species the protoconch (1½ whorl) is regularly spirally micropunctate, while there is no apparent punctation on the succeeding whorls and the apex is not particularly prominent, so there can be little connection between the two, and I can find no mention of this prominent apex and coarse apical micro-punctation in the diagnoses of any other species described from Abyssinia or adjacent districts. The animal is a *Vitrina*, and it is hoped that its anatomy will be published in due course.

VITRINA sp. (?).

Hab. Summit of Mt. Chillalo, 12,000–13,000 ft. (*Scott*).

A single, very small shell, damaged and possibly immature, but in all probability undescribed. Its length is 4·2 mm., and the broken protonoch shows, in a fainter degree, the same micropunctation as the preceding species, but the remainder of the shell is smooth and glossy, pale corneous-yellow.

The animal, however, is in perfect condition and, according to H. Watson, nearly mature; its length, extended in alcohol, is about 6·2 mm. from head to tail; the mantle and whole of the exposed portion of the body is bluish-black, except for a narrow buff stripe along the centre of the sole; the parts of the body contained within the earlier whorls are also buff, becoming darker brown on the last half whorl before the mantle; under a strong hand-lens there is no trace of maculation.

Subfamily *HELICARIONINÆ*.

Genus GRANULARION Germ., 1912.

GRANULARION HIANS "Rupp." (Pfr.).

1848. *Vitrina hians* Rupp., Pfr., P. Z. S. p. 107.

1854. *Vitrina hians* Rupp., Pfr., Conch. Cab. p. 13, pl. i. figs. 45–47.

Hab. Lake Haramaiya (*Scott*).

Hians is the prior name for this common species, which has been awarded other titles, but more material is required before its full synonymy can be established.

Subfamily *SITALINÆ*.

Genus KALIELLA Blanf., 1863.

KALIELLA BARRAKPORENSIS (Pfr.).

1852. *Helix barrakporensis* Pfr., P. Z. S. p. 156.

Hab. Jem Jem Forest (*Omer-Cooper*).

Immature examples, referable to this Indian species, which is so widely distributed over the African continent.

Family HELICIDÆ.

Genus FRUTICICOLA Held, 1837.

FRUTICICOLA STRIGELLOIDES Pollon.

1887. *Fruticicola strigelloides* Pollon., Boll. Mus. Torino, ii. no. 34, p. 2.

1888. *Fruticicola strigelloides* Pollon., Bull. Soc. Mal. Ital. xiii. p. 77, pl. ii. figs. 25-27.

Hab. Zukwala (*Scott*).

The largest of the series is immature, but seems to agree with Pollonera's species.

FRUTICICOLA SCIOANA Pollon.

1887. *Fruticicola scioana* Pollon., Boll. Mus. Torino, ii. no. 34, p. 2.

1888. *Fruticicola scioana* Pollon., Bull. Soc. Mal. Ital. xiii. p. 76, pl. ii. figs. 28–30, pl. iii. figs. 23-24.

Hab. Zukwala (*Scott*); Jem Jem Forest (*Omer-Cooper*).

The fulvous band mentioned in Pollonera's diagnosis is very faint in the shells under notice, but they agree in other respects with his description and figures.

Family ENDODONTIDÆ.

Genus PUNCTUM Morse, 1864.

PUNCTUM CRYOPHILLUM (Mts.).

1865. *Helix* (*Patula*) *cryophilla* Mts., Mal. Blätt. xii. p. 182.

1874. *Helix* (*Punctum*) *cryophilla* Mts., Jick., Nov. Act. k. L.-C. Ak. Nat. xxxvii. p. 54, pl. i. fig. 4, pl. iv. fig. 17.

Hab. Serpent Lake, Wouramboulchi, 9000 ft., 9° N. Lat. and 37° 58′ E. Long. (*Omer-Cooper*).

Family PACHNODIDÆ.

Genus CERASTUS Albers, 1860.

CERASTUS BOCCARDI (Pollon.).

1898. *Buliminus* (*Petræus*) *boccardi* Pollon., Boll. Mus. Torino, xiii. no. 313, p. 7, pl. i. fig. 16.

Hab. Zukwala (*Scott & Omer-Cooper*).

Taking into consideration the great variation in size to which some species of *Cerastus*, notably *retirugis* Mts. and *abyssinicus* Pfr. are liable, there is little doubt that the present series is correctly identified; they are smaller than the type, which was described from Adi-Caié and measures 28 × 14, while they are only about 21 × 11·3 mm. in altitude and diameter, but appear similar to it in all other respects. The convex spire distinguishes them from most of Kobelt's species, though they are very near his *Cerastus malleatus* from the Hakem Mountains, which, however, judging from the figure, may be a synonym of *boccardi*, the elder name.

CERASTUS SACCONII (Pollon.).

1888. *Buliminus sacconii* Pollon., Boll. Mus. Torino, iii. no. 37, p. 3; id., Bull. Soc. Mal. Ital. xiii. p. 66, pl. iii. fig. 8.

Hab. Zukwala (*Scott*).

CERASTUS VIGONII (Pollon.).

1888. *Buliminus vigonii* Pollon., Boll. Mus. Torino, iii. no. 37, p. 3; id., Bull. Soc. Mal. Ital. xiii. p. 65, pl. iii. fig. 7.

Hab. Zukwala (*Scott*).

CERASTUS CHEFNEUXI "Sol." (Bgt.).

1874. *Buliminus abyssinicus* Rupp., Jick., Nov. Act. k. L.-C. Ak. Nat. xxxvii. pl. v. fig. 2 *d*.

1885. *Bulimus chefneuxi* Sol., Bgt., Moll. Choa, p. 12.
Hab. Lake Haramaiya (*Scott*).

Family PUPILLIDÆ.

Genus LAURIA Gray, 1840.

LAURIA WOURAMBOULCHIENSIS, sp. n. (Pl. I. fig. 6.)

Shell very small, ovate, rimate, rather solid and opaque, which may be due to weathering, glossy, pale brown, with darker oblique stripes on the striæ. Spire moderately produced, sides somewhat convex, apex obtusely rounded. Whorls 5, convex, regularly increasing, first 1½ smooth, next 1½ very closely, microscopically, transversely, and slightly obliquely striate in the lines of growth, last 2 sculptured with regular, flattish, somewhat distant, slightly oblique striæ, darker than the intervals between them, there being about 12 and 13 visible on the 4th and 5th whorls respectively; suture simple, well defined. Aperture quadrate, rounded at base, peristome glossy-white, expanded and reflexed, outer lip receding only very slightly in profile, columella erect, margin broadly triangularly reflexed, callus thin, but well marked and continuous; the only dental process is an inrunning parietal plait, inclined downwards to the right, three-quarters of the distance from the columella to the outer lip, but there is a slight inflation of the inner margin one-third way down the outer lip and another, inset and hardly noticeable, half-way up the columella.

Long. 3·3, lat. 2·1; apert. alt. 1·3, lat. 0·8; last whorl 2·0 mm.
Hab. Serpent Lake, Wouramboulchi (*Omer-Cooper*).

The shell is smoother and squatter than *L. bruguierei* and comparatively wider, while the dark transverse stripes impart to it a very distinctive appearance. I find nothing resembling it closely in the fauna of continental Africa, but from the respective figures it must be closely allied to *L. bourbonicensis* Pilsb. (Manual, xxvii. p. 62, pl. viii. fig. 19). The peristome, however, in the Abyssinian race is white and somewhat broadly reflexed, instead of brown and very narrowly so, as emphasised in the case of *bourbonicensis*, which, too, should have stronger sculpture. It has not been proved hitherto that any of the South or Central African Pupillidæ are actually conspecific with those of adjacent lands, and even if *wouramboulchiensis* eventually proves to be merely a variety, it will be entitled to full varietal rank on account of its remarkable striped coloration.

I have not been able to examine the young stage, but it appears hardly likely to belong to a genus other than *Lauria*.

LAURIA BRUGUIEREI (Jick.).

1874. *Pupa bruguierei* Jick., Nov. Act. k. L.-C. Ak. Nat. xxxvii. p. 112, pl. v. figs. 5–6.
Hab. Jem Jem Forest (*Omer-Cooper*).

Family CLAUSILIIDÆ.

Genus CLAUSILIA Drap., 1805.

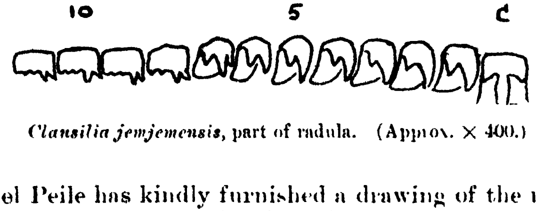
CLAUSILIA JEMJEMENSIS, sp. n. (Pl. I. fig. 5; text-fig. 1.)

Shell rather small, sinistral, fusiform, rimate, fairly solid, glossy with a silken sheen, corneous, the first 3½ whorls yellow-brown, remainder chocolate, mottled with many small, irregular white patches, due to the presence of short white lines on a few adjacent striæ. Spire produced, sides slightly convex, apex rounded. Whorls 7, gradually increasing, the first 4 convex, remainder rather flat, the first 2 showing faint, irregular, microscopic, transverse wrinkles and puckers, remainder covered with close, regular, nearly straight and vertical costulæ, which are continuous on the 3rd and 4th, but become wrinkled and divided by a few spiral furrows on the last three whorls; suture deep, subcrenulate. Aperture obliquely acuminate ovate, peristome white, glossy, continuous and reflexed, dentition consisting of a strong inrunning parietal lamella and two columellar lamellæ, of which the lower is hardly visible from the front, and a very weak plait, slanting inwards and upwards, far within the outer lip on a level with the top of the aperture.

Long. 7·8, lat. 2·1 ; apert. alt. 2·1, lat. 1·3 ; last whorl 3·5 mm.

Hab. Jem Jem Forest (*Omer-Cooper*).

Text-figure 1.



Clausilia jemjemensis, part of radula. (Approx. × 400.)

Colonel Peile has kindly furnished a drawing of the radula, of which the formula is 4.7.1.7.4, but the specimen is not perfect, some lines of marginals being probably missing.

It should be noted that, although they are both pronounced Jum Jum, the Jem Jem of the present expedition is not the Jam Jam of Erlanger, which is situate a considerable distance to the south-east.

In dentition this species belongs to the Abyssinian group which includes *sennaariensis* Pfr., *dystherata* Jick., and *rothschildi* N. & A., while in sculpture and piebald colour-pattern it resembles *degeneris* Preston and *Balea africana* M. & P. It is quite distinct from *sennaariensis*, a more slender species with almost straight, not wrinkled, striæ and no spiral sculpture, while it cannot be assimilated to the description of *rothschildi*, apparently a larger species. Its dimensions are rather near to those of the smaller form of *dystherata* Jick., which measures 7·0 × 1·75 mm., with from 7¼ to 8½ whorls, but Jickeli, a careful author, makes no mention of the spiral furrows or patchy coloration in his species, and particularly emphasises the fact that its aperture slopes backwards in profile, whereas in *jemjemensis* it is vertical, details which appear to provide ample ground for separation.

Of the remaining African Clausiliidæ, *giraudi* Bgt. is a large species with 12 whorls and a length of over 18 mm., while *africana* M. & P. is completely edentulate and *degeneris* Prest., which is smaller than *jemjemensis*, possesses at most but one columellar lamella.

Family STENOGYRIDÆ.

Genus HOMORUS Albers, 1850.

HOMORUS RAGAZZII Pollon.

1887. *Homorus ragazzii* Pollon., Boll. Mus. Torino, ii. no. 34, p. 1.

1888. *Homorus ragazzii* Pollon., Bull. Soc. Mal. Ital. xiii. p. 74, pl. iii. figs. 10, 16.

Hab. Zukwala (*Scott*).

Described from Entoto, Choa.

HOMORUS VARIABILIS (Jick.), var. JICKELII Bgt.

1874. *Subulina variabilis* Jick., form C, Nov. Act. k. L.-C. Ak. Nat. xxxvii pl. v. fig. 2 *d*.

1879. *Subulina jickelii* Bgt., Descr. Div. Moll. p. 10.

1905. *Homorus variabilis* Jick., var. *jickelii* Bgt., Pilsb., Manual, xvii. p. 135, pl. lviii. fig. 48.

Hab. Addis Abeba (*Omer-Cooper*).

The shells agree well with Jickeli's figure, and the eggs are oblong, so the genus must be *Homorus* rather than *Subulina*.

HOMORUS OMERI, sp. n. (Pl. I. fig. 2.)

Shell rather large, subulate, imperforate, extremely thin and glossy, transparent, corneous yellow-brown. Spire produced, sides regular, apex bluntly rounded. Whorls 8½, rather flat, regularly increasing, practically smooth, with only the faintest vestiges of weak transverse wrinkles and close incised spiral sculpture under 50-fold magnification in the freshest specimens; suture simple, shallow, rather oblique. Aperture acutely elongate-ovate, peristome simple, acute, outer lip slightly outcurved and receding to the base, columella very weak, concave, narrowly obliquely truncate near the base.

Long. 30·0, lat. 9·1; apert. alt. 11·2, lat. 5·3; last whorl 17·7 mm.

Hab. Addis Abeba (*Omer-Cooper*).

An extremely fragile, glossy shell, which appears distinct from any described species; most of the Abyssinian *Homori* belong to the typical thick-shelled group of *cyanostoma* "Rupp.," Pfr.

Its nearest relation is *antinorii* Morel., which appears to be conspecific with *vernicosa* Jick., but in *omeri* the whorls increase more rapidly, the last whorl measuring 17·7 mm., whereas in the type of *antinorii*, of almost the same length, it is only 15 mm.

I have great pleasure in naming this fine species in honour of Mr. Omer-Cooper, who has discovered no fewer than six apparently new species in this very interesting district.

Genus SUBULINA Beck, 1837.

SUBULINA CHIARINII Pollon.

1887. *Subulina chiarinii* Pollon., Boll. Mus. Torino, ii. no. 34, p. 2.

1888. *Subulina chiarinii* Pollon., Bull. Soc. Mal. Ital. xiii. p. 74, pl. ii. fig. 31.

Hab. Addis Abeba (*Omer-Cooper*).

Originally collected by Ragazzi at Let-Marefia and Ferere Ghembre.

SUBULINA MUNZINGERI (Jick.)?

1873. *Stenogyra munzingeri* Jick., Mal. Blätt. p. 103.

1874. *Acicula munzingeri* Jick., Nov. Act. k. L.-C. Ak. Nat. xxxvii. p. 133, pl. v. fig. 21.

1908. *Subulina* (*Acicula*) *munzingeri* Jick., Neuv. & Ant., Ann. Sci. Nat. Zool. viii. pp. 304, 305, fig. 18.

Hab. Adda, shore of Hora Harsadi, 8° 52′ N. Lat. and 38° 55′ E. Long. (*Omer-Cooper*).

Two bleached examples from the above locality agree with Neuville and Anthony's figures of specimens from Dire-Daoua, west of Harar, but in all of these the suture is far less oblique than in Jickeli's figure, which appears to represent a more slender form, so it is open to question whether they are correctly identified. The largest shell before me measures: Long. 11·5, lat. 3·0; apert. alt. 2·5 mm., and the whorls are almost flat.

Genus NEOGLESSULA Pilsbry, 1909.

NEOGLESSULA (?) CURTA, sp. n. (Pl. I. fig. 3; text-fig. 2.)

Shell small, acuminate-ovate, imperforate, thin, smooth, glossy, transparent, corneus, pale yellowish-olivaceous. Spire produced, sides very slightly convex, apex bluntly rounded. Whorls 7, flattish, regularly increasing, the first 3 practically smooth, remainder showing very weak, somewhat irregular growth wrinkles, which are closer and slightly recurved just below the suture on the last whorl; suture simple, shallow. Aperture acuminate-piriform, peristome simple, acute, outer lip nearly straight and vertical in profile, columella short, concave, strongly truncate at right angles to its base.

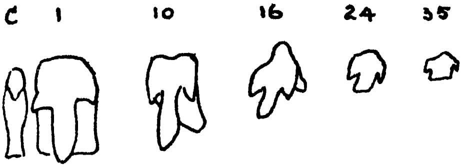
Long. 12·0, lat. 5·2; apert. alt. 4·7, lat. 2·7; last whorl 8·0 mm.

Hab. Jem. Jem Forest (*Omer-Cooper*).

Until its anatomy has been investigated, it is impossible to assign to this species its exact generic position, though it can safely be assumed that *Achatina ariel* Preston and possibly *A. montana* Mts. belong to the same group. Neither *curta* nor *ariel* shows microscopic spiral sculpture on the apex, but in other respects the shell of *curta* resembles closely that of the West Coast *lævigata* Pfr., as do also the radula and external appearance of the animal.

In 1909 Pilsbry * proposed *Neoglessula* as a section of *Glessula* for certain elongate West African forms possessing a spirally engraved apex and strong transverse striation on the later whorls, at the same time leaving *lævigata* in *Glessula* s. s. as having a smooth apex. It is true that *lævigata* differs considerably in form and sculpture from *paritura* Gld. and other members of Pilsbry's section, but it has microscopic embryonal sculpture, consisting of extremely faint, fine, scratchy but regular and continuous spiral grooves, and its radula is nearly akin to that of *paritura* as represented in the Gwatkin Collection in the British Museum.

Text-figure 2.



Neoglessula ? curta, teeth from the radula. (Approx. × 400.)

It has not yet been proved that the true Asiatic *Glessula* exists in Africa, and may be advisable to promote *Neoglessula* to full generic status, placing in it, sensu lato, *lævigata*, *curta*, *ariel*, etc., which will probably be subdivided into one or more sections when their anatomy, for which there is ample material available, has been studied.

The radula formula of the new species, for the figure of which I am indebted to Colonel Peile, is 30.10.1.10.30 × (87 + N.), the outer marginals being either degenerate or rudimentary.

Family SUCCINEIDÆ.

Genus SUCCINEA Drap., 1801.

SUCCINEA HARARENSIS, sp. n. (Pl. I. fig. 4).

Shell rather small, acuminate-oval, imperforate, thin, smooth, semi-transparent, moderately glossy, corneus-amber. Spire short, apex mammillate. Whorls 2, very rapidly increasing, sculptured with broad, weak, transverse growth-striæ, crossed by extremely fine, faint, close microscopic spiral wrinkles; suture oblique, well defined. Aperture ovate, peristome simple, acute, outer lip nearly straight and receding only slightly in profile, columella short, somewhat thickened, extending less than half-way down the aperture, when it forms a slight angle with the rounded inner lip; callus none.

---

* Manual, xx. p. 108.

Long. 7·8, lat. 4·5; apert. alt. 6·1, lat. 3·2; last whorl 7·6 mm.

Hab. Harar (type, *G. Kristensen*); R. Katera, Lake Zwai, 6000 ft. (*Omer-Cooper*).

Type in my collection.

Rather damaged and immature shells from the R. Katera appear to agree with the type of this new species, which has been in my hands for some years awaiting further material prior to its description; the spire is shorter and the aperture longer and broader in proportion than in *rugulosa* and *limicola* Morelet, *striata* Krs., *brumpti* R. & G., *tchadiensis* Germain, and *adowensis*, *chefneuxi*, *meneliki*, *poirieriana*, or *soleilleti* Bgt.

Family VERONICELLIDÆ.

Genus VERONICELLA Blainv., 1817.

VERONICELLA sp.?

1913. *Vaginula pleuroprocta* Mts., Srth., Voeltzkow's 'Reise in Ostafrika,' iii. p. 129.

1918. *Veronicella chevalieri* Germ., Bull. Mus. Paris, p. 117.

Hab. Jem Jem Forest (*Omer-Cooper*).

In the first of the two references cited above, Simroth states that there lies before him a fairly rich series of the group of *Vaginula pleuroprocta* from the travels of Dr. Neumann in Abyssinia, where this group appears to be well developed and to have established a centre; mentioning later that his researches thereon will form the subject of a future work, which, however, does not seem to have materialised.

Omer-Cooper collected two specimens, of which one is probably immature; both are elongate-oval, equally rounded at each end, finely and regularly granulate all over, apart from the footsole, which is transversely grooved. The larger, on the back and tentacles (contracted), is uniform bluish-black, the underside pale buff, closely and somewhat irregularly spotted with dark grey, except for the foot, which is yellowish buff.

Long. (in spirit) 27·2, lat. 10·5; alt. 7·3; footsole 26·0 × 4·3 mm.

The cloacal orifice is 2·6 mm. in length, running obliquely upwards from the point of the foot, parallel to the curve of the tail; the female orifice is on the right side of the animal, half-way between the side of the foot and of the slug, 14 mm. from the front.

The smaller slug is dull reddish-yellow on the back, with four rather irregular rows of broken dark grey lines; underpart and footsole uniform yellow-buff, with a single irregular row of very faint and distant pale grey spots on each side.

Long. 21·0, lat. 9·1; alt. 6·1; footsole 18·5 × 3·4 mm.

The foot narrows gradually from the middle to the rear, and 1·7 mm. from its extremity the sides converge abruptly to form a right angle. Cloacal orifice oblong, 1·1 mm. in length, situate just to the left of the point of the foot, when viewed from beneath, at right angles to the sides; the female orifice is a small oblong dot, 9·8 mm. from the front.

Notwithstanding their different coloration, I imagine that both slugs are conspecific; they are obviously very closely allied to *V. chevalieri* Germ., which was described from near Krebedje, Haut-Oubangui.

Family LYMNÆIDÆ.

Genus LYMNÆA Lam., 1799.

LYMNÆA CAILLAUDI Bgt.

1883. *Limnæa caillaudi* Bgt., Ann. Sci. Nat. Zool. xv. p. 89, pl. x. figs. 100–101.

Hab. Lake Zwai, 8° N. Lat. and 38° 75′ E. Long., 5500 ft. (*Omer-Cooper*).

I give a few synonyms of this widespread species in the faunal list on p. 181, but even after taking all these into consideration, it is impossible to determine the line of demarcation between the intermediates of *caillaudi* Bgt. and *natalensis* Krs., if, indeed, there be any specific difference between them. The short-spired, comparatively obese *natalensis* is the form mainly found in South Africa, and the longer spired, comparatively slender *caillaudi* in the more northern regions, but both occur in company in certain localities, and there is no difference in sculpture.

LYMNÆA TRUNCATULA (Müll.).

1774. *Buccinum truncatulum* Müll., Verm. ii. p. 130.

Hab. Marshes above Serpent Lake, Wouramboulchi (*Omer-Cooper*).

Family PLANORBIDÆ.

Subfamily *PLANORBINÆ.*

Genus PLANORBIS Geoffr., 1767.

PLANORBIS ABYSSINICUS Jick.

1874. *Planorbis abyssinicus* Jick., Nov. Act. k. L.-C. Ak. Nat. xxxvii. p. 215, pl. vii. fig. 21.

Hab. Lake Zwai (*Omer-Cooper*).

PLANORBIS RÜPPELLI Dkr.

1848. *Planorbis rüppellii* Dkr., P. Z. S. p. 42.

1874. *Planorbis rüppellii* Dkr., Jick., Nov. Act. k. L.-C. Ak. Nat. xxxvii. p. 211, pl. vii. fig. 17.

Hab. Small pond in marsh, Hora Abjata, 7° 50′ N. Lat. and 38° 45′ E. Long., 5000 ft. (*Omer-Cooper*).

PLANORBIS HERBINI Bgt.

1874. *Planorbis rüppellii* Dkr , Jick., Nov. Act. k. L.-C. Ak. Nat. xxxvii. pl. vii. fig. 18.

1883. *Planorbis herbini* Bgt., Ann. Sci. Nat. Zool. xv. pp. 91, 101.

Hab. Lake Zwai (*Omer-Cooper*).

I refrain from discussion as to whether the above two species are identical: it is quite easy to separate their shells when they agree with the two figures published by Jickeli, and it will be noticed that they did not occur together in the localities cited above; I possess very typical examples of *herbini* from Harar.

PLANORBIS GIBBONSI Nelson.

1878. *Planorbis gibbonsi* Nels., Q. J. of C. i. p. 379, pl. iv. fig. 3.

Hab. Wouramboulchi; Zukwala; Jem Jem Forest; Lake Zwai; Mt. Chillalo (*Omer-Cooper*).

Subfamily *BULININÆ*.

Genus BULINUS Müll., 1871 (=ISIDORA Ehrn., 1831).

BULINUS NATALENSIS (Krs.)? (Text-figs. 3 & 4.)

1841. *Physa natalensis* Krs., Küst., Conch. Cab. (*Limnæa*), p. 8, pl. i. figs. 12–14.

1883. *Physa natalica* Krs., Bgt., Ann. Sci. Nat. Zool. xv. p. 98.

1908. *Physopsis africana* Krs., N. & A., Ann. Sci. Nat. Zool. viii. p. 267, fig. 5.

Hab. Hora Harsadi, and probably Hora Bishoftu, Adda, and Sucsuci River, L. Zwai (text-fig. 4) (*Omer-Cooper*).

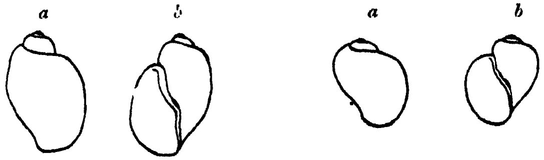
Hora Horeso, Adda, and probably also Hora Bishoftu (text-fig. 3) (*Omer-Cooper*).

It is by no means an easy matter to deal with certain species of *Bulinus* and *Physopsis*, as few authors seem to have studied their microscopic sculpture, a feature which, though perhaps of less value in the determination of aquatic than terrestrial species, must surely be of some importance as affecting the kinship of similar races from mutually remote localities.

In recording *natalica* from Abyssinia, Bourguignat wrote:— "This species, collected in the watercourses of Mt. Zeboul and the plain of the Gallas Raias, is so similar to that of Natal, except for a little smaller size, that it is impossible for me to distinguish between them," and the set from Hora Horeso agree so nearly in form with the South African *natalensis* that there can be little doubt but that they are akin to those examined by Bourguignat, while also agreeing well with Neuville and Anthony's figure, cited above, of a shell from Chola, near Addis Adeba, but not in the least like *Physopsis africana*. The set from Hora Harsadi differ in having a much shorter spire, the outer lip extending almost to the summit, and in the columella being nearly straight, lacking the slight kink half-way down, which is a marked feature in the South African race and, to a less extent, in the shells from Hora Horeso.

When we examine the microscopic sculpture, however, we find that all typical examples of Krauss's species have the first whorl practically smooth, and on the second close, rather strong transverse striæ, which become fainter and much further apart on the third and still fainter on the fourth (last) whorl, with scarcely any trace of spiral sculpture. The same pattern prevails on *B. mutandaensis* (Preston), from Uganda, which I can only consider a synonym of *natalensis*.

Text-figure 3. Text-figure 4.



Bulinus natalensis (Krs.) (?).

Fig. 3.—From Hora Horeso. (× 1.)
Fig. 4.—From Hora Harsadi. (× 1.)

On the other hand, the shells from Hora Harsadi, with similar transverse striation, show faint spiral furrows on the third and fourth whorls, while in those from Hora Horeso the first whorl is evenly punctate, spirally and radially, to the extreme apex, the spirals continuing in strong, shortly-waved grooves, especially strong below the suture, on the remaining whorls.

While the first mentioned of these two races may be conspecific with *natalensis*, it is quite probable that the other is distinct; but there are already in existence so many species of *Bulinus* of which the microscopic sculpture is unrecorded, that I refrain from adding to the number, until it may be possible to enter more fully into the question and determine how much value is attachable to it in the differentiation of aquatic mollusca. The shells from the R. Sucsuci are immature, but it will be noticed that both races appear to live in company at Hora Bishoftu.

Outline drawings of each are given below.

Bulinus schackoi (Jick.).

1874. *Isidora schackoi* Jick., Nov. Act. k. L.-C. Ak. Nat. xxxvii. p. 197, pl. vii. fig. 12.

Hab. Addis Abeba (*Omer-Cooper*).

While the exact relationship of this and the next species to the Egyptian *truncatus* is unsettled, the typical form of *schackoi* is rather distinctive in mature examples; the pair from Addis Abeba agree exactly with Jickeli's figure.

Bulinus sericinus (Jick.).

1874. *Isidora sericina* Jick., Nov. Act. k. L.-C. Ak. Nat. xxxvii. p. 194, pl. vii. fig. 11.

Hab. Serpent Lake and Wouramboulchi marshes; Makke River, L. Zwai, 6000 ft. (*Omer-Cooper*).

This form bears to *truncatus* somewhat the same relationship as does *craveni* Ancey to *tropicus* Krs., in that, in very fresh and slightly immature condition, the shell is strongly lirate, but I doubt whether this constitutes ground for even varietal distinction.

Bulinus truncatus "Fér.", (Aud.).

1827. *Physa truncata* Fér., Aud., Descr. de l'Égypte, i. pt. 3, p. 34.

1922. *Bullinus truncatus* Aud. (=*contorta* Mich., *hemprichii* and *brocchii* Ehrn., cum var. *approximans* Mouss., *maresi*, *raymondiana*, *brondeli* Bgt., *schackoi* and *sericina* Jick., *lirata* Mouss., *dybowskii* Fisch., *innesi* Palry. and *tiberiadensis* Prest.), Annandale, Ind. Journ. Med. Res. x. p. 484.

Hab. Wouramboulchi; water-hole north of Makke R. (*Omer-Cooper*).

The waters of Wouramboulchi connect with the Blue Nile, so there may be some significance in *truncatus* and *sericinus* being found close together there.

Bulinus forskali (Ehrn.).

1831. *Isidora forskalii* Ehrn., Symb. Phys., Evert., 3rd species (no pagination).

Hab. Sucsuci River, south of Lake Zwai (*Omer-Cooper*).

PELECYPODA.

Genus Sphærium Scop., 1777.

Sphærium pharaonum "Bgt.," Palry.

1909. *Sphærium* (*Corneola*) *pharaonum* Bgt., Palry., Mém. Inst. Ég. vi. p. 74, pl. xi. fig. 14.

Hab. Marshes above Serpent Lake, Wouramboulchi (*Omer-Cooper*).

Except for having very slightly weaker, though similar, sculpture, this series agrees well with the Nilotic species.

SPHÆRIUM SUBCAPENSE Bgt.

1874. *Cyclas capensis* Krs., Jick., Nov. Act. k. L.-C. Ak. Nat. xxxvii. p. 291, pl. xi. fig. 14.

1881. *Sphærium subcapense* Bgt., Ann. Sci. Nat. Zool. xv. p. 133.

Hab. Wouramboulchi (*Omer-Cooper*).

I am a little doubtful as to the correctness of this identification, but the shells agree with Jickeli's measurements and in sculpture and fragility with his description.

Genus PISIDIUM C. Pfr., 1821.

PISIDIUM PIROTHI Jick.

1881. *Pisidium pirothi* Jick., Jahrb. D. Mal. Ges. p. 340.

Hab. Serpent Lake, Wouramboulchi; Addis Abeba (*Omer-Cooper*).

This unfigured and little-known species is the only *Pisidium* yet recorded from Abyssinia, having been described from Harasa, between Atbara and Bassalam. Omer-Cooper's examples correspond with Jickeli's measurements, and appear to agree with his rather scanty description; the cardinal tooth of the right valve is of rather regular crescent-shape, as emphasised by the German author in the case of *pirothi*.

3. A Survey of the Molluscan Fauna of Abyssinia.

The following list includes every recent species of land and freshwater mollusc, except for a few instances of obvious misidentification, which has been attributed to Abyssinia or Eritrea in the appended bibliography, and may be regarded as practically complete. I give details of synonymy only when it has been established by other authors.

Ptychotrema denticulatum (Morel.), and varr. *quinqueplicata* (=*papillifera*) and *hildebrandti* Jick., *hamacenica* Bgt. and *nana* Conn.
Ptychotrema raffrayi (Bgt.).
„ ***roberti*** (Prest.).
Gulella meneliki (Prest.).
„ ***simplicima*** (Prest.).
„ ***somaliensis*** (Smith).
„ ***turennei*** (N. & A.).
Raffraya milne-edwardsi Bgt.

Vitrina abyssinica Rüpp., Pfr.
„ ***antonellii*** Pollon.
„ ***bianchii*** Pollon.
„ ***caillaudi*** Bgt.
„ ***conquisita*** Jick.
„ ***darnaudi*** Pfr.
„ ***demissa*** Jick.
„ ***devexa*** Jick.
„ ***giuliettii*** Pollon.
„ ***grossepunctata*** Conn.

Vitrina helicoidea Jick.
„ *herbini* Bgt.
„ *humilis* Pollon.
„ *isseli* Morel.
„ *jamjamensis* Mlldff.
„ *jickelii* Krs.
„ *mamillata* Mts.
„ *martensi* Jick and varr. *haliotoidea* Pollon. and *planulata* Jick.
„ *milne-edwardsiana* Bgt.
„ *modesta* Pollon.
„ *raffrayi* Bgt.
„ *ragazzii* Pollon.
„ *riepiana* Jick.
„ *semirugata* Jick.
Africarion lymphaseus (Morel.).
„ *palleus* (Morel.).
Granularion hians Rupp., (Pfr.).
„ *ruppellianus* (Pfr.).
Helicarion erlangeri Kob.
„ *raffrayi* Bgt.
„ *ragazzii* Pollon.
Gudeella abyssinica Jick. (=*euryomphala* Bgt.).
„ *oleosa* (Pfr.) (?).
„ *unguinosa* (Pollon.).
„ *restii* (Jick).
Ledoulxia alfieriana Sol., (Bgt.).
„ *bloyeti* (Bgt).
„ *elatior* (Mts.).
„ *filomarginata* (Kob.).
„ *pyramidea* (Mts.).
„ *rothschildi* (N. & A.).
„ *zeltneri* (R. & G.).
Kaliella barrakporensis (Pfr.).
Sitala raffrayi Bgt.
„ *steudneri* (Jick.).
„ *trochulus* Pollon.
Limas sidamoensis R. & G.
Agriolimax abessinicus Srth.
„ *afer* Srth.
„ *concrementosus* Srth.
„ *deckeni* Srth.
„ *fuscus* Srth.
„ *gardullanus* Srth.
„ *gimirranus* Srth.
„ *glandulosus* Srth.
„ *gofanus* Srth.
„ *jickelii* (Heynem.).
„ *kaffanus* Srth.
„ *kontanus* Srth.
„ *koschanus* Srth.
Agriolimax limacoides Srth.
„ *uataderensis* Srth.
Atoxon erlangeri Srth.
Patula abyssinica Jick.
Punctum abbadianum Bgt. (=*brocchii* Jick., *non* Calcara.
„ *brucei* Jick.
„ *cryophillum* (Mts.).
Eremina desertella (Jick.).
Xerophila hamacenica (Bgt.).
„ *subnivellina* (Bgt.).
Fruticicola assaortina Pollon.
„ *beccarii* (Jick.) (=*ciliata* Morel, *non* Venetz.).
„ *combesiana* (Bgt.).
„ *darnaudi* (Pfr.).
„ *dhericourtiana* (Bgt.).
„ *ferretiana* (Bgt.).
„ *galinieriana* (Bgt.).
„ *herbini* (Bgt.).
„ *heuglini* (Mts.).
„ *isseli* (Morel.) (=*achilli* and *lejeaniana* Bgt.).
„ *pilifera* (Mts.).
„ *rosenbergi* (Prest.) and var. *depressa*.
„ *scioana* Pollon.
„ *strigelloides* Pollon.
Conulinus affinis (Prest.).
„ *macroconus* (Bgt.).
„ *subeminulus* (Bgt.) (=*eminulus* Morel., 1872, *non* 1848).
Cerastus abbadianus (Bgt.).
„ *abyssinicus* Rüpp., (Pfr.) (=*ilqi* Bgt).
„ *achilli* (Bgt.).
„ *antinorii* (Pollon.).
„ *boccardi* (Pollon.).
„ *carolinæ* (Kob.).
„ *chefneuxi* Sol., (Bgt.).
„ *daroliensis* (Kob.).
„ *erlangeri* (Kob.).
„ *galinierianus* (Bgt.).
„ *gara-mulatæ* (Kob.).
„ *harrisi* (Rve.).
„ *hemprichi* (Jick.;.
„ *herbini* (Bgt.).
„ *jickelianus* (Nev.).
„ *lejeanianus* (Bgt.), *fide* Kobelt.
„ *lycanianus* (Innes).
„ *malleatus* (Kob.).
„ *meneliki* (Bgt.).
„ *neumanni* (Kob.).

Cerastus olivieri (Pfr.).
,, *raffrayi* (Bgt.).
,, *rothschildi* (N. & A.).
,, *rüppellianus* (Kob.).
,, *sacconii* (Pollon.).
,, *scioanus* (Pollon.).
,, *simonis* (Bgt.) (= *sinuosus* Bgt., Prest., *lapsus calami*).
,, *soleilleti* (Bgt.).
,, *tanisierianus* (Bgt.)
,, *vigonii* (Pollon.).
Rhachistia erlangeri (Kob.).
,, *galanensis* (Kob.).
,, *moluensis* (Kob.).
,, *rhodotænia* (Mts.).
,, *rochebruniana* (Bgt.).
,, *rorkorensis* (Kob.).
Pupoides sennaariensis (Pfr.) (= *cerealis* Palad., *ragius* Jouss., *æthiopicus* and *maharasicus* Bgt.).
,, *vermiformis* (Palad.).
Laura bruguierei (Jick.).
,, *wouramboulchiensis* Conn.
Pupilla globulosa (Jick.).
,, *raffrayi* Bgt.
Orcula imbricata (Jick.).
Gastrocopta haggenmacheri (Jick.).
,, *hermosa* (Jouss.).
,, *klunzingeri* (Jick.).
,, *pleimesi* (Jick.).
Nesopupa bisulcata (Jick.).
Negulus abyssinicus (Reinh.).
,, *reinhardti* (Jick.).
Truncatellina blanfordi (Jick.).
,, *lardea* (Jick.).
,, *schilleri* (Jick.).
,, *similis* (Jick.).
Acanthinula peracanthoda (= *raffrayi*) Bgt.
Abbadia ethiopica Bgt.
Clausilia dystherata Jick.
,, *jemjemensis* Conn.
,, *rothschildi* N. & A.
,, *sennaariensis* Pfr.
Limicolaria abajensis Kob.
,, *adansoni* (Pfr.).
,, *beccarii* Morel.
,, *burtoniana* Grandid.
,, *caillaudi* (Pfr.).
,, *candidissima* Parr., Shutt.
,, *choana* Bgt. (= *pyramidalis*, *glandinopsis* and *chefneuxi* Bgt. and var. *flamminifera* N. & A.).
Limicolaria dhericourtiana Bgt.
,, *flammata* (Caill.) and var. *smithi* Pilsb.
,, *flammea* (Müll.) and var. *globosa* Germ.
,, *gestroi* Germ.
,, *heuglini* (Mts.) and var. *jickelii* Pollon.
,, *jickeliana* Prest.
,, *kordofana* Parr. (Phil.).
,, *rüppelliana* (Pfr.).
,, *soleilleti* Bgt.
,, *spekiana* Grandid.
,, *vanattai* Pilsb.
Achatina daroliensis Kob.
,, *erlangeri* K. & M.
,, *scheinfurthi* Mts.
,, (*Leptocallista*) *raffrayi* Jouss. *fide* Kob.
Homorus angustatus (Jick.).
,, *antinorii* (Morel.).
,, *cyanostoma* Rupp., (Pfr.).
,, *ellerbecki* Kob.
,, *erlangeri* Kob.
,, *gara-mulatæ* Kob.
,, *ginirensis* Kob.
,, *obesus* Kob.
,, *omeri* Conn.
,, *perlucida* (Prest.).
,, *perrierianus* (Bgt.).
,, *princeps* Prest.
,, *ragazzii* Pollon.
,, *rothschildi* (N. & A.).
,, *suaveolans* (Jick.).
,, *subulatus* (Jick.).
,, *variabilis* (Jick.) and varr. *jickelii* and *lhotelieri* Bgt.
,, *vernicosus* (Jick.).
Subulina chiarinii Pollon.
,, *erlangeri* Bttg.
,, *isseli* Jick.
,, *lacuum* Bttg.
,, *mabilliana* Bgt.
,, *meneliki* Prest.
,, *munzingeri* (Jick.).
,, *newtoni* Gir.
,, *nympha* Prest.
,, *vicina* Prest.
Opeas gracile (Hutt.).
,, *indifferens* Bttg.
Neoglessula (?) *ariel* (Prest.).
,, *curta* Conn.
,, *montana* (Mts.).
Cecilioides isseli (Palad.).

Cecilioides soleilleti (Bgt.).
Cœlestele ægyptiaca Bgt.
„ *paladilhiana* Nev. (=*Francesia scalaris* Palad.).
Zootecus insularis (Ehrn.) (=*adenensis* Pfr.) and var. *major* N. & A.
Zua (?) *thalassina* Jouss.
Succinea æthiopica Bgt.
„ *baumanni* Stur.
„ *brumpti* R. & G.
„ *chefneuxi* Bgt.
„ *debilis* Morel.
„ *hararensis* Conn.
„ *limicola* Morel.
„ *meneliki* Bgt.
„ *rugulosa* Morel. (= *adowensis* and *poirieriana* Bgt.).
Veronicella comoriensis Fisch.
Lymnæa caillaudi Bgt. (= *æthiopica*, *acroxa*, *alexandrina*, and *raffrayi* Bgt. and *africana* Rupp., (Bgt.)).
„ *exserta* Mts.
„ *gravieri* Bgt.
„ *natalensis* Krs.
„ *orophila* Morel.
„ *soleilleti* Bgt.
„ *truncatula* (Müll.).
Planorbis abyssinicus Jick.
„ *adowensis* Bgt.
„ *æthiopicus* (= *angulatus*) Bgt.
„ *alexandrinus* Ehrn.
„ *boccardi* Pollon.
„ *boissyi* P. & M.
„ *bozasi* R. & G.
„ *cecchii* Pollon.
„ *ehrenbergi* Beck (= *cornu* Ehrn.).
„ *gibbonsi* Nels.
„ *herbini* Bgt.
„ *ruppelli* Dkr.
„ *stanleyi* Smith (= *bridouxianus* Bgt.).
„ *sudanicus* Mts.
Segmentina angusta Jick.
Bulinus coulboisi (Bgt.).
„ *forskali* (Ehrn.) (=*fischerianus* Bgt.).
„ *natalensis* (Krs.).
„ *schackoi* (Jick.).
„ *sericinus* (Jick.) and var. *harpula* Poll.
„ *tchadiensis* (Germ.).
„ *truncatus* Fér., (Aud.) (=*contortus* Mich. & *brocchii* Ehrn.).
Physopsis abyssinica Mts.
„ *africana* Krs., *fide* N. & A.
„ *eximia* Bgt.
„ *meneliki* Sol., Bgt.
„ *soleilleti* Bgt.
Ancylus abyssinicus Jick.
„ *hamacenicus* Bgt. (= *compressus* Jick., *non* Nyst.).
Ligatella daroliensis Kob.
„ *ganalensis* Kob.
Pila bridouxi (Bgt.).
„ *ovata* (Oliv.) and var. *kordofana* Parr., (Phil.).
„ *revoili* (Bgt.).
„ *wernei* (Phil.).
Lanistes carinatus (Oliv.).
„ *ovum* Ptrs., Trosch.
Viviparus abyssinicus (Mts.).
„ *unicolor* (Oliv.).
Cleopatra bulimoides (Oliv.).
„ *pauli* Bgt.
„ *percarinata* Bgt.
„ *pirothi* Jick.
„ *soleilleti* Bgt.
Melanoides tuberculatus (Müll.).
Bulimus goryi (Bgt.).
„ *neumanni* (Mts.).
„ *sennaariensis* (Pfr.).
„ *subbadiellus* (Bgt.).
Assiminea æthiopica Thiele.
Valvata nilotica var. *scioana* Pollon.
Theodoxus africanus Parr., (Rve.).
Unio abyssinicus Mts.
„ *æneus* Jick.
„ *chefneuxi* N. & A.
„ *dembiæ* Rssmlr.
„ *hamyanus* Bgt.
„ *ilqui* Sol., Bgt.
„ *jickeli* Simps.
„ *meneliki* Sol., Bgt.
„ *rothschildi* N. & A.
„ *soleilleti* Bgt.
„ *traversii* Pollon.
Spatha alfieriana Bgt.
„ *bloyeti* Bgt.
„ *bozasi* R. & G.
„ *brumpti* R. & G.
„ *caillaudi* Mts.
„ *marnoi* Jick.
Mutela angustata Sow., (Rve.).
„ *nilotica* (Sow.).
„ *rostrata* (Rang.).
Etheria elliptica Lam. (= *caillaudi* Fér., *tubifera* Sow., and *nilotica* Let., Bgt.).

Corbicula callipyga Bgt.
„ *consobrina* (Caill.).
„ *fluminalis* (Müll.) and var. *crassa* Mts.
„ *gravieriana* Bgt.
„ *pusilla* Parr. (Phil.).
„ *soleilleti* Bgt.
Sphærium abyssinicum Pollon.
„ *boccardi* Pollon.
Sphærium pharoanum Bgt., Palry.
„ *subcapense* Bgt. (= *capense* Jick., *non*. Krs.).
Soleilletia abbadiana Bgt.
„ *hamyana* Bgt.
Eupera jickelii (Bgt.).
„ *parasitica* Parr., (Desh.).
Pisidium pirothi Jick.

A study of the foregoing list, which contains no fewer than 218 so-called species of terrestrial and 102 of aquatic mollusca, will show that this Abyssinian fauna is remarkable both for its richness and extreme exclusiveness, since of the terrestrial species there appear to be only twelve, exclusive of *Limicolaria*, which are known to exist outside the confines of Abyssinia and Eritrea, and some of these were described from the adjacent district of Sennaar, while others are either widely distributed or may have been wrongly determined.

The explanation of this exclusiveness lies in the fact that Abyssinia is a country of elevated plateaux and mountains, well supplied with lakes and rivers, verdant, at least in the rainy season, yet cut off from other regions of a like character by the arid, low-lying lands which surround it, such as Somaliland, Gallaland (the south-eastern district of Abyssinia). and the Sudan. Though Abyssinia is well within the Tropics (about 4½° to 14½° N. Lat.), its climate on the high plateaux is temperate. Almost all round its boundaries the mountains rise steeply, and in some parts form a veritable wall. The distance by rail from Jibuti in French Somaliland to Addis Abeba, the capital of Abyssinia, is only 490 miles, yet the rise from sea-level is more than 8000 ft., the first day's journey out of Somaliland reaching a plateau of nearly 4000 ft.

Most of Eritrea is in the Abyssinian faunal preserve, as the boundaries are purely political, and owing to the difficulty of determining the exact localities mentioned by certain authors, I have admitted all the Eritrean, except the semi-marine, mollusca into my list. But the Red Sea coast of Eritrea, as well as Jibouti and all French Somaliland and the coastal regions of British Somaliland, are not really within the Abyssinian area, and the difference between the land-shells is very marked.

Due, no doubt, to this temperate tropical climate is the prevalence of such northern genera as *Fruticicola* and *Agriolimax*, which do not appear to be endemic further south, and the abundance of *Vitrina*, which extends in both directions, while, on the other hand, Abyssinia is such a veritable stronghold for the tropical genus *Cerastus* that it may well have originated there. Another noteworthy feature of the land-shells is the practically complete absence of the operculates, while, with one or two individual exceptions, this country marks the northern limit of

Ledoulxia, *Gudeëlla*, *Homorus*, *Subulina*, and the Streptaxidæ. With the exception of *Zootecus insularis* the Arabian influence, which is so strongly marked in Somaliland, is not apparent.

With regard to the freshwater mollusca, after eliminating more than a third of the existing species as unnecessary, there will remain no very remarkable feature; perhaps *Planorbis abyssinicus* Jick. and, in less degree, the same author's *Bulinus schackoi* are more local in their occurrence than the rest; I have not traced records of them outside Abyssinia.

4. Bibliography.

The appended list includes all the principal works dealing more or less exclusively with the recent mollusca of Abyssinia. I have omitted several short preliminary papers by various authors, in cases where these were subsequently incorporated in their more comprehensive productions cited below.

(i.) Morelet, A.—Notice sur les coquilles terrestres et d'eau douce recueillies sur les côtes de l'Abyssinie. Ann. Mus. Genova, iii. 1872, pp. 180–208, pl. ix.

(ii.) Jickeli, C. F.—Fauna der Land- und Süsswasser-Mollusken Nord-Ost-Afrika's. Nov. Act. k. Leop.-Carol. Deutsch. Akad. Naturf. xxxvii. 1874, pp. 1–352, pls. i.–xi.

(iii.) Bourguignat, J. R.—Description de diverses espèces et genres de l'Égypte, de l'Abyssinie etc. Tremblay, Paris, 1879, pp. 1–54.

(iv.) Jickeli, C. F.—Land- und Süsswasser-Conchylien Nordost-Afrika's gesammelt durch J. Piroth. Jahrb. D. Mal. Ges. viii. 1881, pp. 336–340.

(v.) Bourguignat, J. R.—Histoire malacologique de l'Abyssinie. Ann. Sci. Nat. Paris, Zool. xv. 1883, 162 pp., pls. vii.–xi. and Avis à intercaler à la suite de l'Histoire etc. Tremblay, Paris, 1883, pp. 1–3.

(vi.) Bourguignat, J. R. Mollusques terrestres et fluviatiles recueillis par M. Paul Soleillet dans son voyage au Choa, Éthiopie Méridionale Tremblay, Paris, 1885, 48 pp., 1 pl.

(vii.) Pollonera, C.—Molluschi dello Scioa e delle Valle del l'Havash. Bull. Soc. Mal. Ital. xiii. 1888, pp. 49–86, pls. ii.–iii.

(viii.) Jousseaume, F.—Espèces terrestres de Massaouah, de Perim et d'Aden, etc. Bull. Soc. Mal. Fr. vii. 1890, pp. 81–102, pl. iii.

(ix.) Pollonera, C.—Molluschi Terrestri e fluviatili dell' Eritrea raccolti dal Generale di Boccard. Boll. Mus. Torino, xiii. 1898, no. 313, 13 pp., 1 pl.

(x.) de Angelis d'Ossat, G., & Millosevich, F.—Seconde Spedizione Bottego, Studio Geologico, 1900, pp. 147–153, pl. iii.

(xi.) Simroth, H.—Ueber die von Herrn. Dr. Neumann in Abessinien gesammelten aulacopoden Nacktschnecken. Zool. Jahrb. xix. 1903, pp. 673–726, pls. xxxix.–xlii.

(xii.) Germain, L.—Sur quelques Mollusques terrestres et fluviatiles rapportés par M. Ch. Gravier du Desert Somali. Bull. Mus. Paris, 1904, pp. 344–354.

(xiii.) Rochebrune, A. T. de, & Germain, L.—Mollusques recueillis par la Mission du Bourg de Bozas. Mem. Soc. Zool. Fr. xvii. 1904, pp. 5–29, pls. i.–ii.

(xiv.) Neuville, H., & Anthony, R.—Contribution à l'étude de la faune malacologique des lacs Rodolphe, Stéphanie et Marguerite. Bull. Soc. Philom. Paris, viii. 1906, pp. 275–300, pl. xii.

(xv.) Neuville, H., & Anthony, R.—Récherches sur les mollusques d'Abyssinie. Ann. Sci. Nat. Paris, Zool. viii. 1908, pp. 241–340, pls. iii.–v.

(xvi.) KOBELT, W.—Die Molluskenausbeute der Erlangerschen Reise in Nordost Afrika. Abh. Senckenb. Naturf. Ges. xxxii. 1909, pp. 1–52, pls. i.–xi.

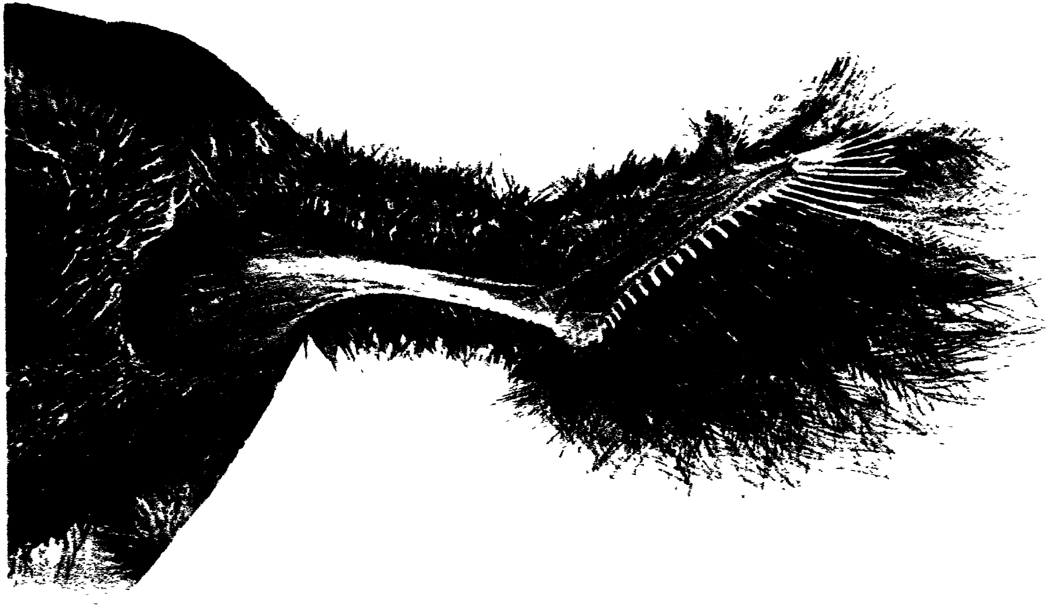
(xvii.) PRESTON, H. B.—Notes on and Additions to the Terrestrial Molluscan Fauna of Southern Abyssinia. Proc. Malac. Soc. ix. 1910, pp. 163–170.

(xviii.) CONNOLLY, M.—On a Collection of Mollusca from Southern Abyssinia. Proc. Zool. Soc. London, 1928, pp. 163–184, pl. i.

EXPLANATION OF THE PLATE.

Fig. 1. *Vitrina grossepunctata* Conn. Shell (× 2) and microscopic apical sculpture (highly magnified).
2. *Homorus omeri* Conn. (× 2.)
3. *Neoglessula* (?) *curta* Conn. (× 2.)
4. *Succinea hararensis* Conn. (× 4.)
5. *Clausilia jemjemensis* Conn. (× 6.)
6. *Lauria wouramboulchiensis* Conn. (× 10.)

P Z. S. 1928, LOWE, Pl. I.



John Bale, Sons & Danielsson, L^{td}

UNDER SURFACE OF WING OF RHEA CHICK.

11. Studies and Observations bearing on the Phylogeny of the Ostrich and its Allies. By PERCY ROYCROFT LOWE, B.A., M.B.Cantab., F.Z.S.

[Received October 19, 1927: Read February 7, 1928.]

(Plate I.*; Text-figures 1–22.)

CONTENTS.

	Page
Introduction	185
Distribution in Space and Time	191
The Pterylar Coat	197
Feather Structure	199
The Aftershaft	207
The Question of the Patagium	208
The Fore Limb	210
The Coraco-scapular Bar	223
The Palatal Region	232
The Quadrate Bone	235
The Sternum	235
The Sternal Callosity	238
The Vertebral Column	238
The Intestinal Tract	240
The Ventricular Moderator Band	241
The Syrinx	241
Phylogenetic Status	242
Some Conclusions	244
List of Works Referred to	245

INTRODUCTION.

While engaged in the study of the struthious assemblage of birds, I became increasingly certain that while such terms as "Dromæognathous" or "Palæognathous" might justifiably be used to designate a comprehensive group of birds possessing a primitive form of palate which sharply differentiates them from the Euornithes or Neognathæ, characterised on their part by the possession of a more highly developed or derived palate, such terms were inapplicable when used solely in reference to the struthious group, since it is evident that there are certain primitive fossil types, such, for example, as *Gastornis*, *Dasornis*, and *Remiornis*, which, although they may have been Palæognathous, may not necessarily have been Struthious.

It seems clear, in fact, that by such terms as Palæognathæ or Neognathæ two *subclasses* of birds are implicit, and that if we wish to specify the struthious *order* another term must be employed. By the struthious order is here understood such an assemblage as is formed by the Emus, Cassowaries, Kiwis, Moas,

---

* For explanation of the Plate, see p. 247.

Rocs (Æpyornithidæ), Ostriches, and Rheas, in addition to such fossil forms which have been, or will be, found to be properly associated with it. To such an assemblage or order the term "Struthiones" may well be applied.

The question whether this assemblage of differing families may, indeed, be rightly regarded as a natural group has been the subject of much difference of opinion and will be considered later (see p. 242), as it would appear to have a bearing on what will, perhaps, be regarded as the principal theme of this paper, viz., the primary flightlessness of the Struthiones.

It will be noticed that the Tinamous are not included in the struthious order. I have given a great deal of attention to the position of this group and its relation to the Struthiones, and the conclusion I have come to after a first-hand study of every branch of its anatomy is that the Tinamous possess one series of characters which may be described as Palæognathous but which may not necessarily be struthious, another series solely confined to such structures as are intimately connected with the functions of flight and which may be described as "Neognathous," and other characters which do not quite conform to either of these divisions. It seems evident, therefore, that the Tinamous represent a primitive group (Crypturi) which can neither be included with the Palæognathæ nor with the Neognathæ. They are almost exactly intermediate, in fact, between the two.

A somewhat comprehensive study of the Struthiones, fossil recent and embryological, carried out from time to time during the last two or three years, has had the effect of convincing me that in this group we have to deal with birds which are the more or less specialized representatives of a primitive stock which never acquired the power of flight.

All the evidence, so far as I can interpret it, seems to point to the strong probability that the degree of "flying power," if such an expression is permissible, exhibited in the wings of the ostrich and rhea represents the actual high-water mark attained by any known representatives of the group, and that the Struthiones must be regarded as a blind-alley offshoot descended independently of any other order and directly from the ancestral bird.

A number of proofs which appear to support this view will be brought forward in the present paper, but as the results of these investigations seem to call for a radical change of view from that generally adopted, it seems necessary to show, first of all, what is the general belief which has been commonly held. In regard to this there seems to be little doubt that the true position of the Struthiones in relation to the rest of the avian class has been misinterpreted, so strongly and persistently misinterpreted, indeed, that there seems good justification for a review of the whole question.

Thus, so far as one can gather from a study of the literature, the general consensus of opinion among zoologists, ornithologists, and palæontologists would appear to be that this group of ostrich-like birds, commonly known as the "Ratitæ," is a degenerate or retrogressive group descended from some proto-carinate ancestor which could fly. Over and over again, for instance, one finds in the papers studied a persistent tendency to interpret the many primitive morphological characters so constantly met with in terms of degeneracy, while the group as a whole is portrayed as the ancient relic of a primitive stock whose descendants have *lost* the power of flight.

Thus it is the "loss" of flight, the "loss" of the keel, the "loss" of continuity in the mechanism of the wing-feathers which seem to have been again and again insisted upon, while all the anatomical and histological features, which bear the hall-mark of the reptile or point to a phase of avian evolution which might almost be termed embryonic, seem to have been ignored.

That the above is not an exaggerated view of the opinions which have been held in the past will, I think, be evident from the following quotations.

Owen (1866, ii. p. 43), for instance, says:—"Although as a general rule in the class Aves the separate bones [of the skull] can be discerned only at an early period, yet in these birds *in which the power of flight is abrogated* [italics mine] the indications of the primitive centres of ossification endure longer, and in the species here selected (the ostrich) for the illustration of the cranial segments, the constituent bones of the skull have been merely separated by maceration in the half-grown bird." A statement which not only implies a loss of flight in the struthious ancestor but might possibly be interpreted to mean that the delayed union of the cranial sutures was associated with the abrogation of flight, whereas it is, of course, obvious that Owen must have recognised it as a belated manifestation of a reptilian character in the "Ratite" skull. We know at any rate that the delayed union of the cranial elements brings the Struthiones into close touch with a group of reptiles which did not fly.

Jeffery Parker (1882, p. 255), in some remarks on flightless birds in general and the "Ratitæ" in particular, regards the latter as "the greatly specialised but degenerate descendants of carinate birds"; and again further on (p. 256) he says: "The Proto-Carinatæ being by this hypothesis good fliers were presumably not of gigantic size; moreover, they probably possessed feathers with connected barbs so that the special characters of the Ratite plumage should be looked upon as a secondary or degenerate, not an ancestral character." In passing I may state that this structural aspect of the feathers is dealt with further on (pp. 199–207), where I think conclusive evidence is brought forward to prove that in the matter of feather-structure in the Struthiones we are dealing with a primary condition and one which sheds a good deal of light on the primitive feather.

Beddard (1898, p. 493), again, in his 'Structure and Classification of Birds,' after defining the struthious order, says: "As will be seen from the above definition the characters of this group are to a considerable extent negative characters. They are for the most part such characters as are correlated with the loss of the power of flight. We need not, therefore, lay too much stress upon them as indicative of the naturalness of the group."

A few lines further on he again speaks of the osteological peculiarities as *degeneration*, and says: "perhaps even the osteological and other characters which, as already suggested, are but evidence of the loss of flight-power, may be of more importance as an argument for affinity than is generally admitted; it may show that they are allied because the degeneration has proceeded along the same lines."

Gadow regards the Struthiones as a group of primitive forms more nearly representing Proto-Carinatæ than any other living birds.

Pycraft (1898, p. 260), in his important paper on the "Morphology and Phylogeny of the Palæognathæ," says: "It is now generally admitted that the Palæognathæ must be descendants of the avian Proto-Carinate form capable of flight"; while on p. 222, in his remarks on the pectoral arch, he regards the shoulder-girdle of the flightless Palæognathæ as having undergone considerable modification and as bearing evidence throughout of retrogression. Quoting Jeffery Parker from his "Observations on the Anatomy and Development of *Apteryx*," he says that authority has given a number of characters which lend the strongest support to the view as to the derivation of the Palæognathæ from an avian Proto-Carinate form capable of flight. "To many," he says, "they will be convincing." The most important of these are:—

"The fact that the skeleton of the fore-limb is that of a true wing.

"The presence of an alar membrane or patagium.

"The presence of remiges and tetrices majores."

"The alar membrane," he goes on to say, "is a structure of great significance. According to Parker it is the remnant of a once extensive scale-covered patagium. As these scales gradually became transformed into feathers the size of the patagium decreased."

These points, and more especially that concerning the presence of a patagium, will also be taken up again (p. 208), but I may say here that I have examined embryos of all the existing Ratitæ, more especially the Rhea, of which I was fortunate enough to obtain a fine series in different stages of development from Colonel Morley Knight, and I can find no indication of any patagium at all.

In the same paper on the *Apteryx*, from which Pycraft quotes, Jeffery Parker says (p. 37): "On the whole it appears to me that the structure of the wing of *Apteryx* lends support to the view that the Ratitæ are the descendants of birds which possessed the power of flight, a view which, I believe, Owen was the first to advance. In spite of Miss Lindsay's conclusions [1885, p. 684] from her study of the development of the sternum, and Wray's [1887, p. 343] from his researches on the wing, I am still disposed to think that the balance of evidence is in favour of the hypothesis to which I was led by a study of the flightless Rallidæ, that the Ratitæ spring from a Proto-Carinate stock, a theory which has recently received strong support from the researches of Fürbringer and Gadow."

Both these last two authors consider that the present Ratitæ are the descendants of birds which once possessed the power of flight. Yet Gadow remarks (1888, p. 666) that "the Penguins retain a condition [of the remiges and coverts] which in other birds is referred to their embryonic life, whilst *Struthio* represents an intermediate stage." He makes, however, the proviso that no secondary reduction from several to one series of under wing-coverts has taken place—a reduction, however, which he assumes in *Rhea*. On the other hand, he points out that Wray (1887, p. 354) has shown that *Struthio* shows various conditions which in the Carinatæ are repeated during their embryonic growth only.

Coming down to more recent times, Broom (1906), in a paper on the embryonic development of the ostrich's shoulder-girdle, also thinks the ancestor of this bird flew, and by inference that the Palæognathæ have lost the power of flight, while some of the anatomical features exhibited by them are evidence of retrogression. Broom's embryological researches will be again referred to in another part of this paper dealing with the shoulder-girdle (see pp. 223 232).

Finally, Professor J. E. Duerden (1920), who has had exceptional opportunities of studying the ostrich in South Africa, has devoted a paper entirely to the "Methods of Degeneration in the Ostrich." Apart from various forms of retrogression or specialization in the ostrich, such as the reduction of the number of the toes, examples which no one is likely to deny, it is clear that Duerden regards the inability of the ostrich or its ancestors to fly as a secondary phenomenon due to the *loss* of various factors, for he says (p. 131) "the loss of effective barbicels, leaving the vane of the feather loose and open and incapable of offering resistance to the air, has rendered flight impossible. Probably as a result of the same degenerative tendency, other losses of plumages have taken place as well as a total loss or reduction in the size of the wing, the disappearance of a sternal keel, and of elements from the shoulder-girdle." Under the heading of "Feather Structure" (p. 199) I shall bring forward evidence which seems to me to go a long way towards definitely proving that the feathers of the entire group of present-existing Struthiones never got so far forward in development as to produce barbicels at all, or even barbules in any way comparable with those of volant birds. No one seriously thinks that the present-existing genus *Struthio* ever flew, although many are of the opinion that its ancestors did. But it is interesting in this respect to remember that we can go back to the Upper Eocene of the Fayûm district in Lower Egypt and, in the case of *Eremopezus*, rest convinced from the evidence of fossil remains that this bird was, practically beyond doubt, a large non-flying courser which in general make-up was probably comparable with the large struthious forms of the present day. If this is so the process of degeneration of such a minute and delicate structure as the "struthious barbicel" would appear to have extended over an unconscionably long time.

In the meantime enough has been said to make it clear that there has always been a very strong tendency to regard the ostrich-like group of birds as the degenerate descendants of some primitive stock possessed of the power to fly.

In the present paper evidence will be brought forward which seems to me to point to the strong probability that this primitive group had no volant ancestor, and that flight in any way comparable to that exhibited by modern birds had never been attained by them.

Furthermore, degeneration or retrogression, although doubtless present in the wings of certain groups, such as the Cassowary, Emu, Kiwi, Moa, or *Æpyornis*, seems to have played but a very secondary part in the history of these the most primitive of living or comparatively recently-extinct birds, a fact which will, I believe, become plainly evident when we come to deal with the microscopical details of the feathers or go deeper to investigate the structural peculiarities and development of the shoulder-girdle, sternum, and other structures too numerous to refer to here.

On the contrary, there seems to be strong reasons for coming to the conclusion that in the Struthiones we have a cumulative mass of evidence which appears to the writer to point overwhelmingly not to the fact of retrogression or degeneration, so much insisted upon by other writers, but to a primitive arrest of development, which can only be explained on the hypothesis that as a group or phylum they failed at the very outset to attain to the full fruition of avian development. Thus it hardly matters to what structure or organ we turn but we are met with a condition of morphological evolution which can only be described as either never having proceeded much beyond an embryonic or early stage in avian evolution or as being frankly reptilian.

To use a somewhat hackneyed expression we seem to be confronted with a series of "living fossils," which present us with a picture of at least one phase of early avian life not far removed from the very earliest or dinosaurian.

The question whether flight has been lost or not seems, unfortunately, to have loomed too largely in past speculations, obscuring other and more important evidence bearing on the history of this interesting group of birds; but, at any rate, it seems extremely difficult to see how the mere loss of flight or the mere diminution of the fore-arm, a diminution not unknown in the Theropodous dinosaurs, apart from any question of flight, could have possibly had the effect of leaving in its trail so many structural sequelæ of a primitive character as occur in the Struthiones.

Finally, I might add here that it seems to have been generally, if not universally, held that most flightless birds *lost* their ability to fly in consequence of their restriction to insulated areas of land, where, owing to the absence of carnivora or other foes, there was no incentive to fly in an easy-going existence, flight being therefore lost by default.

It will be noted under the heading of "The Fore-Limb" that in the case of the Kiwis, Moas, Cassowaries, Emus, and Rocs (*Æpyornis*), I take an opposite point of view and suggest that these insulated areas represent the only place where these primarily flightless birds or their fossil remains were likely to have been preserved in any great numbers—that, in a word, they represent the last sanctuaries which enabled these relics of a primitive fauna to hold out for so long through geologic periods to which they were not in reality adapted, and that by inference it was only a specialization towards a swiftly cursorial habit of life which enabled the Ostrich and the Rhea to withstand the rapidly developed carnivorous fauna of the Tertiary.

DISTRIBUTION IN SPACE AND TIME.

In regarding the struthious group as the derelict remnants of a Proto-Carinate ancestry it seems more than probable that their very wide distribution in space and time has too often been forgotten, if not overlooked, while their occupation of restricted areas has been greatly emphasized.

Rothschild (1910), in a paper read before the 5th International Ornithological Congress held at Berlin, expressed the opinion "that the ratite Palæognathæ did not begin to develop to any large extent until very late, for before the Pleistocene epoch the number of species is very small." It seems questionable, however, if a false impression may not have been produced by (1) the scantiness of fossil records in the main continental land-masses, that is to say, in geographical areas other than those marking the relics of the ancient "Antipodea" and "Lemuria," where absence of carnivora may have contributed in no small degree to the abundance of fossil remains actually found; and (2) the depression undergone by land areas formerly corresponding to the more extensive distribution of such forms as the Emu, Cassowary, Moa, and Kiwi, a depression which led to a large degree of isolation with consequent specific diversity on a large scale or, as in the case of Moas, to great overcrowding, possible hybridization, and wholesale extinction.

But in any case we have undoubted evidence of Palæognathine, if not actually struthious, forms existing as far back as the

Eocene and onwards, so that as regards at least the later Miocene and early Pliocene there is enough fossil evidence to make it a matter of certainty that the Ostrich ranged from the Mediterranean basin as far eastwards as China, and as far north as Mongolia (*Struthiolithus*), with a probable southerly extension into Africa, whose exact limits at that period have yet to be defined. There seems no doubt, in fact, that the Palæognathæ have overrun the earth since at least Eocene times, while a comparative study of the osteological features characterising its far-flung component groups renders it almost certain that their history antedates that period by a very considerable time.

It may be useful, therefore, to give a short epitome of the present and former distribution of such struthious forms as are known. Starting with the present epoch we have the Rhea distributed over a very large part of the South American continent, two well-differentiated genera (*Rhea* and *Pterocnemia*) and at least three species being met with. In Africa we have four species of Ostrich (*Struthio*) ranging over practically the whole extent of the continent with the exception of the forested equatorial zones; while a subspecies of the Northern *Struthio camelus* is still found in the Syrian and Arabian deserts. If, too, we appeal to historical records (Yule, 1921, ii. p. 437) this area of distribution of the Ostrich can almost certainly be extended to Persia, Turkestan, and the Persian Gulf, though very doubtfully indeed to India.

Another widely ranging group is the Casuarii, occupying almost the whole of the Papuan subregion and Australia. Of the genera represented, *Casuarius* is confined to the Papuan subregion and North Queensland, and of this single genus Lord Rothschild has recently defined no fewer than sixteen species and seventeen subspecies. *Dromæus*, on the other hand, with three species, is confined to Australia and Tasmania.

Passing over to New Zealand we meet with the interesting group of Kiwis (Apteryges), which there seems good reason to think must have formerly had a less restricted area of distribution than at present, since the Kiwi, in the probably more generalised form of *Metapteryx bifrons* (De Vis, 1891, p. 448), has been found fossil in the Pleistocene of Queensland; while coming within the scope of historical times we get the Moas (Dinornithes), which have been subdivided into seven genera, *Dinornis*, *Megalapteryx*, *Anomalopteryx*, *Cela*, *Emeus*, *Pachyornis*, *Palæocasuarius*, and many species. Most of the fossil material relating to the Moas has been derived from either recent or Pleistocene beds, but *Anomalopteryx* has been found in deposits said to be Pliocene, while two or three papers have been written describing fragments of *Dinornis* bones found in New Zealand in deposits older than those in which they usually occur (Forbes, 1891).

Finally, we come to the Rocs (Æpyornithes) of Madagascar, which may reasonably be considered to have survived to well within the age of *Homo sapiens*, and probably to within the historical period. Three genera, *Æpyornis*, *Mullerornis*, and *Flacourtia*, have been described, of which the first is distinguished by having had eleven species referred to it, so that, as in the case of New Zealand and the Moas, there can hardly be a doubt that Madagascar represented a last stronghold or sanctuary for the remnants of a formerly more widely-distributed and continental species. Judging from the wing-bones *Æpyornis* may have been a slower-moving bird than *Struthio*, so that on the invasion of the African continent by its present fauna it seems conceivable that it found conditions altogether too adverse, conditions which did not exist in its last insular retreat. Its legs also were thick and heavy, so that probably they were an additional handicap in a struggle against an invading carnivorous fauna.

While, therefore, it seems probable that *Struthio* was derived from a Eurasian source (Pikermi and Siwalik fauna), and that it invaded the African continent along with its present mammalian fauna, it may have taken the place of the Æpyornithes, of which the last remnant, almost literally torn from the continent, was preserved in the shrinking mass now known as Madagascar. It is true, of course, that there is little or no actual fossil evidence to support the idea that the Æpyornithes inhabited Africa before the advent of *Struthio*, so that the above suggestion is purely conjectural. Nevertheless, the strongly mineralised fragments of the huge struthious egg described by Andrews (1910) as *Psammornis rothschildi* may well have been Æpyornithine, especially if, as suggested by Andrews, they had originally been brought up from a well of considerable depth near which they were found about twenty miles east of Touggourt in Southern Algeria. So much, then, for a brief review of the distribution of the "Ostriches" in recent times.

If, now, we endeavour to get a view of the past history of the group we find the *Rhea* described from fossil remains in beds which have been determined as Pleistocene and Pliocene, as, for example, *Rhea fossilis* (Ameghino, 1891, p. 448), *Rhea subpampeana* (Moreno & Mercerat, 1891, tab. xx.), and *Heterorhea dabbenei* (Rovereto, 1914, p. 160).

As regards the Ostrich, eggs have been found fossil in South-east Russia and North-east China belonging to a form considerably larger than *Struthio*, known as *Struthiolithus chersonensis* (Brandt, 1873); also in the Fayûm region of Lower Egypt; in South and East Algeria, all in strata which have been regarded as Pleistocene; while Père Teilhard de Chardin (1926) has found fragments of ostrich eggs beneath the hearths of Palæolithic man in Ordos (Choei-tong K'eou), China.

In the Hipparion beds in the island of Samos the ostrich occurs in a form known as *Struthio karatheodoris* (Major, 1888); in the Siwaliks of North India in beds slightly more recent it occurs as *Struthio asiaticus* (Milne-Edwards), while Mecquenem (1918, p. 54) has recorded fossil remains (phalanx) from Maragha (Persia) in strata of the same age as those in Samos.

J. G. Andersson (1923, p. 71) has recorded that Dr. Wiman reports finding the pelvis of a large ostrich among material from the Hipparion beds at locality 30, T'ai Chia Kon, in North-west Shansi on the Yellow River (North-west China). Finally, R. C. Andrews (1926) reports finding both Pliocene and Pleistocene remains of "*Struthiolithus*" in Mongolia, north of the Altai Mountains, thus apparently confirming Andersson's records for Northern China.

Coming to the Upper Eocene we have fragments of the distal end of the tibio-tarsus of an "Ostrich" from the Fayûm district of Lower Egypt described by Andrews (1904, p. 168) under the name of *Eremopezus eocœnus*. In passing we would call attention to the following interesting note made by Andrews in his original description of this ancient "Ratite" form: ". . . . it may be remarked that the existence of a true Ratite so long ago as the Eocene makes it at least possible that some of the main groups of the Ratitæ may have had a common ancestry *and are not the results of separate retrogressive modifications leading to the loss of flight, with the various correlated changes*." (Italics mine.) A few lines further on, however, he goes on to say: "There is, however, another possibility that must not be lost sight of, and that is that after all *Eremopezus* may be merely another instance of retrogressive modification leading to the loss of flight and increase of bulk in a group of carinate birds such as has occurred in the case of the *Stereornithes*, the *Gastornithes*, and probably in most of the early so-called Ratite birds." But, we may ask, can this be reconciled with his remark upon the generalized nature of the fragment of the tibio-tarsus found (p. 170), where he says "comparing this specimen with the tibio-tarsus of the other Ratites, it may be said that to some extent it combines the character of several of them," as, for instance, *Rhea*, *Æpyornis*, and *Struthio*? Moreover, as he says, it seems clear that this bird differs widely from the other Ratites and certainly from any of the Carinatæ.

Passing to Basal Eocene deposits we find *Gastornis* (Hébert, 1855, p. 579) in both the London and Paris basins, but whether this a truly struthious form, some more generalised Palæognathous forerunner, or some primitive form on an independent co-lateral line seems to be open to doubt. *Dasornis londiniensis* has also been described by Owen (1869, p. 59) from the Basal Eocene of the Isle of Sheppey, and *Remiornis*, whose "coracoid is essentially of the Ratite type," by Lemoine from the same horizon in France (Cernay).

Another fossil relic whose reference to this horizon is, however, doubtfully established has already been referred to as the form described by Andrews as *Psammornis rothschildi* from fragments of what once must have formed part of a huge egg comparable in size to those of *Æpyornis*.

Passing eastwards again we find that several species of fossil Emus have been discovered in Australia in strata described as

Pleistocene or recent, *Dromæus patricius* (De Vis, 1888, p. 1290, pl. xxxvi.), *D. gracilipes* (De Vis, 1891), *D. queenslandiæ* (De Vis, 1884. p. 27, pls. iv. v.), while of the Cassowary group we have the following: *Casuarius* sp., obtained from Pleistocene deposits in New South Wales and described by Lydekker (1891, p. 354), and *Hypselornis sivalensis*, described by the same author (1891, p. 354), from the Pliocene of the Siwalik Hills in North-west India.

Then we have two gigantic forms of a group *Dromornis* which was probably allied to the *Casuariinæ*. These were respectively described by Owen (1872, p. 682) and by Lydekker (1891, p. 356) from the Pleistocene of Queensland and from auriferous deposits at a depth of 200 feet in strata described as Pliocene. Finally, another form, known as *Genyornis newtoni* and described by Stirling and Zietz (1896), is recorded from the Pleistocene of South Australia.

Summary of Distribution.

With the possible exception of *Remiornis*, *Dasornis*, and *Gastornis* all the forms mentioned in the above review seem to be definitely deserving of inclusion among the Struthiones proper.

It is only comparatively recently that we have begun to realise that the present distribution of the Ostrich (*Struthio*) by no means corresponds with its former areas of distribution, and the same applies to a less obvious extent to other groups of the Struthiones. For example, the fossil record is proving more and more definitely and surely that even as lately as Palæolithic times the Ostrich existed in China, its remains having been found in the hearths of Palæolithic man.

Going still farther back to the Upper Miocene, its former area of distribution apparently stretched westwards from China to the Mediterranean in a probably continuous belt or zone, which corresponded with that of the Hipparion fauna with which, doubtless, it associated, just as the present-day ostrich does or did with the antelopes of the South African fauna (text-fig. 1). At this period the African continent, in whole or part, may or may not have been populated with the struthious ancestors of the present-day Ostrich. Later on it was to be invaded, along with its present mammalian fauna, by *Struthio*. At any rate, it is certain from fossil evidence that in the Lower Eocene period some generalised form of Ostrich lived somewhere in the area now known as the Fayûm district of Lower Egypt.

This wide distribution both in time and space, the success in migrating from one wide area to another, seems to negative the possibility of *Struthio* being a degenerate carinate. When, too, in addition, we reflect that from a survival point of view *all* the other far-flung world-wide struthious groups have been nearly equally successful and that they have undergone almost precisely the same series of so-called "degenerative changes" in their make-up—that is to say, however widely separated by oceans, they exhibit almost identical and unmistakable morphological characters of a nature obviously primitive, we may well pause to ask if their true status in relation to the other avian orders has not been misinterpreted (see also p. 242).

Text-figure 1.

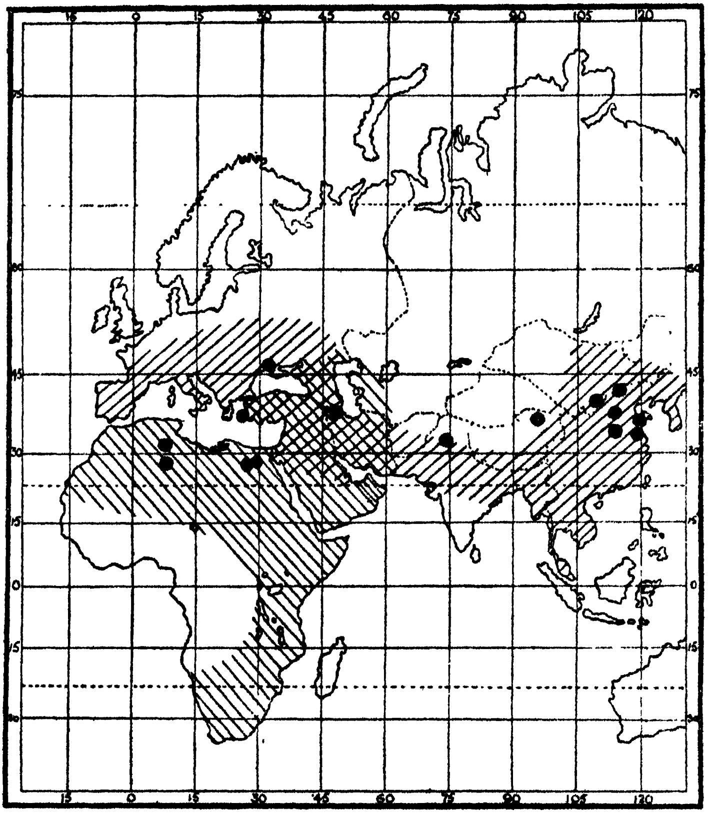

15
0
15
30
45
60
75
90
105
120
75
60
45
30
15
0
15
30

FIG. MAP TO ILLUSTRATE PAST AND PRESENT DISTRIBUTION OF THE OSTRICH

▧ PRESENT DISTRIBUTION OF OSTRICH
▨ DISTRIBUTION OF HIPPARION FAUNA
● LOCALITIES OF FOSSIL STRUTHIOUS REMAINS

An enumeration of actual specific forms comprising the known living and extinct forms of "true Ratite Palæognathæ" is given by Lord Rothschild (1910, pp. 150–155), and is no less impressive than their distribution in space and time, amounting as it does to ninety-one, exclusive of subspecies. Lord Rothschild's "true

Ratite Palæognathæ" is, for all practical purposes, identical with my Struthiones, and it is necessary to once more seriously ask ourselves if such a formidable toll of specific forms can be reconciled with the idea of a degenerate assemblage.

THE PTERYLAR COAT.

Nitzch (1867), Miss Lindsay (1885, pl. xliii. figs. 6 & 7), Jeffery Parker (1891, pp. 35, 36), Pycraft (1898, pp. 150–162), and others, have described the pterylar coat and its apteria in the Struthiones, and I do not propose to occupy much space in going over this ground. Since, however, the observations of most of these writers may have given the impression that the once prevailing idea that the feathers in this group of birds are evenly distributed over the body in what is practically a continuous coat is not one in accordance with facts, I take this opportunity to state that my studies of embryos have led me to the conviction that the old idea is the more correct one.

It seems indeed difficult to avoid the conclusion that the pterylar coat of the flightless Struthiones represents a primitive generalised phase of the Neognathous coat with all its definitely contrasted feather-tracts and bare spaces.

Pycraft (*l. c.* pp. 150, *et seq.*) has stated that the description of the feather-tracts in the Struthiones is most easily accomplished by an enumeration of the apteria or bare spaces. When, however, one comes to analyse his description of these and, by a sort of inverse process, the corresponding pterylæ (pp. 150–162), the apteria resolve themselves into three, viz., a spinal, a mesogastric, and a lateral trunk space—*Apt. spinale*, *Apt. mesogastræi*, and *Apt. laterale*—while practically the only feather-tract enumerated is the *Pteryla alæ*.

I have examined the pterylosis of all the existing Struthiones in embryos taken from the egg, and my conclusions are as follows:—

1. *Apt. spinale.*—In *Dromæus*, *Casuarius*, and *Apteryx* there is not the faintest indication of any apterion at all. In *Struthio*, from the level of the head of the humerus posterad to the level of the head of the femur, there is on either side of the mid-line (spinal ridge) an *indication* of an apterion, which might be described as the first beginnings of the bare space. In *Rhea* there are two extremely narrow apteria—an anterad and a posterad—on either side of the mid-line covering much the same extent but separated, as Pycraft has rightly pointed out, by an area in which the feathers overlap the middle line.

The above arrangement is just what one might have expected, for *Dromæus*, *Casuarius*, and *Apteryx* are in other respects more primitive than the more specialised *Struthio* and *Rhea*.

2. *Apt. Mesogastræi.*—As its name implies this so-called apterion is situated on the mid-line of the under surface of the body. In *Dromæus*, *Casuarius*, *Struthio*, and *Rhea* it represents

to my mind nothing more than the space occupied by the sternal callosity in its embryonic phase of development. There is no hint of any bare area either anterad or laterad of the margins of the callosity, while the posterad extension corresponds to the handle of the racket-shaped figure assumed by this structure and does not seem to extend further in the embryo than the yolk-sac.

In *Apteryx* there is the same racket-shaped bare space which possibly marks a once existent callosity.

3. *Apt. trunci laterale.*—This is not, to my mind, a very fortunate term to have applied to the apterion concerned, for it represents in the embryos of the struthious forms enumerated above the under surface of the wing, which is absolutely devoid of feathers, and a corresponding bare space on the trunk, which I think might more happily be described as the axilla (*cf.* Pl. I.).

In nearly all the papers which I have consulted on the subject of pterylosis the impression seems to have been conveyed that it is only in *Struthio* that the under surface of the wing is absolutely bare of under wing-coverts and feathers. I find that in the embryos of *Rhea*, *Dromæus*, *Casuarius*, and *Apteryx* it is also bare, even in quite well-developed embryos, and this equally in *Rhea*, in which it is commonly said that there is one row of under wing-coverts represented, a statement which is only true so far as the adult is concerned. Every other part of the body, whether head, neck, legs, or trunk, in all these embryos which I have enumerated, is for all practical purposes one uniform coat of feathers; and the conclusion which it seems legitimate to draw is that the pterylar coat of the existing Struthiones represents a primitive covering which existed in birds in general before the acquisition of flight.

Moreover, a study of the so-called feather-tracts and bare spaces (where they exist) in the embryos of the Struthiones seems to render it obvious that their arrangement or evolution has not advanced to a level, or even along lines which can be said to be in any way comparable with the degree of development or specialization, attained in a corresponding stage of growth in the modern Neognathæ, whether volant or non-volant. So that, even if in some of the Neognathæ, as for instance in the ducks, divers, and auks, we allow that the arrangement of the pterylar coat is of an especially adaptive character, it seems impossible to resist the conclusion, firstly, that the Neognathine pterylosis is one which has been evolved in obvious correlation with the function of flight; while, on the other hand, we have in the Palæognathæ a primitive generalised or simple method of disposition of the contour feathers in which it seems impossible to observe any such connection with this function.

It seems, too, equally difficult to regard the undifferentiated homogeneous feather coat of the Struthiones as degenerative in the sense that the ancestors of the "ratite" forms possessing it would have originally exhibited a more specialised pterylar tract system adapted to the function of flight, for had they done so it seems probable that we should have had presented to our view in the flightless Struthiones of the present day some remnants or evidences of tracts homologous with, or even analogous to, the tracts with which we are familiar in the Neognathæ. But of such remnants there does not appear to be the faintest evidence.

A further word must be said about another striking peculiarity in the pterylar arrangement of the flightless Struthiones, a point alluded to above, viz., that this group differs from the Neognathæ in having the under surface of the wing entirely naked in the embryo.

Wray (1887, p. 353) has pointed out the strong probability that in *carinate* birds one or two rows of under wing-coverts have migrated from the dorsal aspect of the wing, where they were originally situated, and this supposition is supported by the fact that during the growth of the embryo the two hindermost rows of coverts are pushed round from the dorsal to the ventral aspect of the wing, carrying with them a fold of skin at the same time. Thus, in the embryo bird, as Wray points out, the feather rudiments first appear on the dorsal aspect of the wing, so that the naked condition of the under surface of the "struthious" wing would appear to represent a very early phase of avian development; or, as Wray again suggests, the adult Ostrich's and Rhea's wings are survivals of the above-mentioned transition stage of the avian wing and have probably never been used for flight, having undergone special modifications of their own.

Pycraft (1898, p. 170), on the contrary, explains the naked under surface of the Palæognathous wing as being a secondary feature due to the suppression of the feathers by the long continued application of the wing to the side of the body, having apparently overlooked the fact that the Ostrich and Rhea barely move a yard, however slowly, without an associated uplift of the wing, and that the application of the wing to the body is no more continuous than in such a bird as a Rail or a Partridge, if indeed as much.

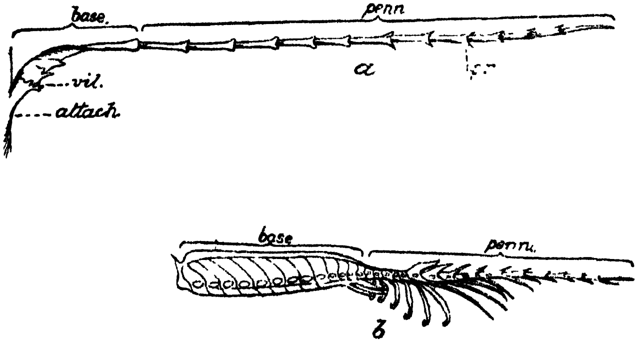
FEATHER STRUCTURE.

It is, however, when we come to a study of the actual structure of the feathers in the struthious chick and adult that we are struck with the full force of the conviction that we are dealing with a primitive and not a degenerate condition. Perhaps the most obvious feature is the complete absence of any pennaceous structure of the wing, tail, or contour feathers. This condition is constant in the genera *Dinornis*, *Apteryx*, *Dromæus*, *Casuarius*, *Struthio*, *Rhea*, and *Pterocnemia*, a fact which I have verified for myself by microscopical examination. Thus this character, by which is meant that there is no adhesion of the barbs and barbules to one another to form feather vanes, sharply differentiates, as has been generally admitted, the Palæognathous feather from the Neognathous. What, however, does not appear to have been so generally realised by such well-known writers as Jeffery Parker, Gadow, Pycraft, Beebe, Duerden, and others is that this complete absence of any interlocking mechanism is correlated with a corresponding absence of the teleoptylic or final phase of evolution of the feather characteristic of the Neognathæ.

In the absence, therefore, of the final or teleoptylic phase of feather evolution characteristic of the volant wing, it is obvious that *vestiges* of hamuli and barbicels, so often alluded to by authors, cannot possibly be present, a point which by itself alone seems to indicate that these authors do not appear to have fully realised the fundamental difference which distinguishes the Palæognathine from the Neognathine feather in the adult phase.

So far as I have been able to gather from a perusal of the literature of the subject, Chandler (1916) appears to be the one apparent exception who has definite doubts as to the secondarily derived nature of Palæognathous plumage, for he says (p. 287): "If the contour feathers of Ostriches are *not* derivatives of pennaceous feathers, then Ostriches are not descendants of flight birds and their striking primitive characters need not be looked upon as secondarily acquired. The absence of plumules, filoplumes, and aftershafts, the even distribution of feathers over the entire body and the similarity of the neossoptiles to the teleoptiles, as well as the general form of the barbules, all suggest the possibility of the Ostriches not being derived from birds with pennaceous feathers and therefore not from flight birds."

Text-figure 2.



a. Down barbule, diagrammatic and greatly enlarged. After Chandler.
b. Distal barbule of a teleoptylic feather, diagrammatic and enlarged. After Chandler.

To show the difference in structure, and division into base and pennulum with fila (*pr.*) and hooklets, etc.

At any rate, I think it will be obvious from the evidence adduced below that this absence of pennaceous structure in the

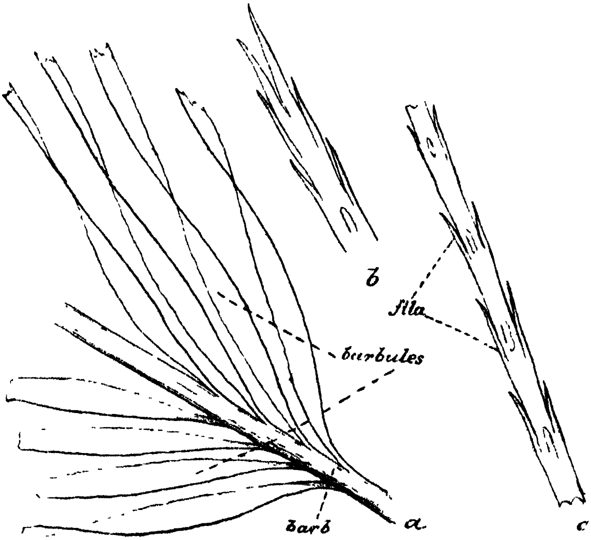
Struthiones is not due to any degeneration, of which there does not appear to be any indication, but to the fact that in the evolution of the Palæognathine feather the final phase of the modern carinate or Neognathine feather was never attained. What, in a word, seems to have happened was that evolution got no further than a stage which corresponds to the downy prepennal phases seen in the chicks or juveniles of carinates, except that in such genera as *Struthio* and *Rhea* there is a degree of specialisation of the downy structure which surpasses what occurs in the other struthious genera. It is obvious, moreover, that the struthious barbule, whether specialised or generalised, regarded from the point of view of a volant structure entirely missed its mark, and, in fact, in its specialised form might well be regarded as having proceeded on an independent side-line. For instead of a condition of feathering in which the barbs or rami are arranged in closely adpressed parallel rows and with barbules highly specialised for the purpose of maintaining a close interlocking of their constituent parts, as in the remiges of any flying carinate bird, we have what is recognised as a "discontinous" arrangement, not only of the barbs or rami but of the barbules or radii. Moreover, in these latter we have, as has just been indicated, either (1) a more generalised or primitive phase in which, whether the barbule is taken from the chick or adult (or from whatever part of the body, wing, or tail), the structure of the base and pennulum differs in no essential, or even noticeable way from that observed in the barbule of any normal down feather—a condition of things which I have noted in *Apteryx*, *Dromæus*, *Casuarius*, and *Dinornis* (no feathers of the chick of this last are known), or, on the other hand, (2) a more specialised condition of this downy structure as in *Struthio* or *Rhea*.

As regards category 1, a glance at the accompanying text-figures (3, 4, and 5) seems to be all that is necessary to appreciate the actual structure of the barbules in the several groups.

As regards category 2, in *Struthio* the barbule again presents no essential difference in structure in chick or adult or from whatever part of the body it may have been taken. Instead, however, of having the normal histological features of a down barbule the individual cells or nodes have been obviously developed or specialized, so that under a low power (text-fig. 6) the barbule appears as a narrow, flattened, ribbon-like structure which has apparently undergone a considerable amount of keratinisation. In the adult this latter process has so affected the base that the individual cells have largely lost their identity, but towards the distal end or pennulum the cell structure and fila (nodes and internodes) are easily observed. A reference to the accompanying text-figures (6 and 7) will, it is believed, make these points clear without further wearisome description; but a special point to be noted here is that barbules, whether belonging to the proximal or distal row, are of equal length and spring from the barb at exactly the same angle and level. In other words, they have just the same disposition as is to be noted in the barbules of a down-like feather. Their discontinuous arrangement is also obvious.

Another important point to be noted concerns the fila springing from the cells towards the distal end (pennulum) of the struthious barbule (*cf.* text-fig. 7). Whatever opinion we may hold as to the potentiality *originally* possessed by these fila to develop into the barbicels or hooklets (hamuli) characteristic of the volant armature of the carinate feather, one thing seems to me almost beyond dispute, viz., that they are *not* degenerate or vestigial structures. Pycraft (1898, p. 167) has, on the other hand, described the distal end of each barbule or radius in the Ostrich as bearing fila disposed as in normal Neognathæ, but none, he says, is sufficiently elongated to form hooklets, *although they are probably vestiges of these* (italics mine).

Text-figure 7.



Ostrich (*Struthio*). Barb from adult remex showing (*a*) bases of barbules springing from barb, much keratinized. *b.* and *c.* Details of pennulum showing nodes and fila. All greatly enlarged.

Apart, however, from what has been stated above, a comparison of the structure of the distal end of the struthious (*Struthio*) barbule in the chick and adult seems alone sufficient to refute the view that these fila are vestigial barbicels or hamuli; for although I have already said that, so far as essential features are concerned, the barbules of young or old are not to be differentiated, it is apparent that there is a sufficient advance in development of the distal cells in the transition from the chick to the adult, as there is also in the differentiation between the structure of the base and pennulum. It comes, in fact, to this, that these down-like fila on the distal end (pennulum) of the Ostrich barbule are no more to be regarded as vestiges of barbicels with their hamuli than are the fila of any ordinary down barbule. Moreover, the barbules are themselves uniformly and regularly discontinuous, as they are throughout the whole group, so that even if hamuli and barbicels had been originally present it is difficult to see how they could possibly have functioned, or how and why barbules from being continuous could or should have become discontinous. Even in the down-like barbules of *Dinornis*, *Apteryx*, *Dromæus*, and *Casuarius* there seems to me an indication of an evolution *inter se* in an upward direction towards a more and more specialised structure; at any rate, in tracing a series in the order named there is no evidence of any degenerative process, so that there seems to be no escape from the conclusion that the fila and cells which go to make up the distal end (pennulum) of the struthious barbule, far from being degenerate or retrogressive vestiges of the carinate cilia or hamuli and their appropriate cells, are simply the modified or specialised fila and cells of the original down-like barbule.

On the other hand, so far as my studies have led me, there is no flightless struthious form in which the barbules, whether taken from the chick or adult or from whatever part of the bird —wing, tail, or body—even approximate in structure to the similar barbules of a volant carinate form, while I doubt if they could conceivably be taken for anything else than a down barbule either simple or specialised (*cf.* text-figs. 2-7).

To regard the struthious barbule as a retrogressive derivative of the volant carinate barbule seems not only unjustified by the evidence, but the fact that it has been generally so regarded has led perhaps more than anything else to what I believe to be a complete misconception of the past history of these, the most primitive living birds.

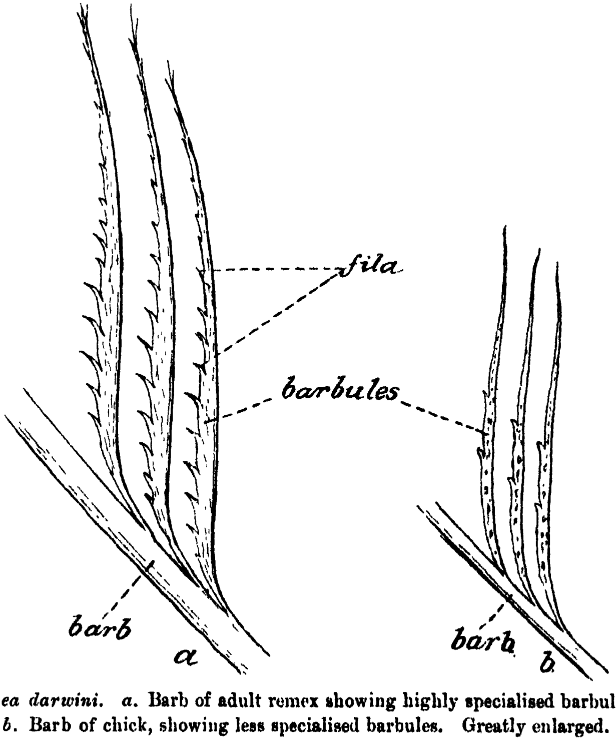
There are other points which go to substantiate what has already been said, for example:—

1. In the Struthiones there is no essential difference between the structure and arrangement of the nestling and adult barbs and barbules. The only exception that I have been able to discover exists in the Rheas, in which the barbules of the wing-feather of the chick are more definitely down-like than in the adult, although not so purely down-like as in a form like *Apteryx*, while in the barbule of the adult Rhea there is a considerable degree of specialisation leading to a condition of feather structure which neither approximates to down nor to the carinate barbule, but reflects in some degree certain details of the discontinuous barbule to be noted in the contour feathers of carinates in the juvenile phase (*cf.* text-fig. 8). In the Rhea, therefore, we appear to have a condition of evolution of the feather more advanced

than in all the other struthious forms. In the Ostrich, on the other hand, over-specialisation seems to have put the barbule definitely out of court from the point of view of any chance it may have had of developing into a volant barbule. In *Dinornis*, *Apteryx*, *Dromæus*, and *Casuarius* we may still see it in its primitive down-like form.

2. As has been incidentally referred to above, it is now recognised that the barbules of the struthious barb differ from those of the Neognathæ in the important fact that the distal and proximal rows are of equal length and spring from the barb at exactly the same angle. The specialised barbules of the Ostrich, for example, from whatever part of the body they are taken or whether examined in the chick or adult stage, spring at exactly the same divergent angle on either side of the barb and at the same level. It seems inconceivable that such a simple arrangement which exactly reflects that of down could have been derived from the highly specialised arrangement present in the volant

Text-figure 8.



Rhea darwini. *a*. Barb of adult remex showing highly specialised barbules. *b*. Barb of chick, showing less specialised barbules. Greatly enlarged.

feather. They are, too, of equal length. A close examination of the barbules in the adult *Dinornis*, *Apteryx*, *Dromæus*, and *Casuarius* discloses just the same conditions; but in these forms the structure of the barbule is so purely down-like that it seems difficult to believe that anyone could seriously hold the view that it is a secondary effect of degeneration from a previously volant phase.

3. Finally, it may be stated here, as has already been noted by others and confirmed by Chandler, that plumules and filoplumes are conspicuous by their absence in all the existing Struthiones. It therefore follows from what has been said above that the only type of feathering that we are left with is a prepennal down-like plumage, for as the Ostrich and the other struthious nestlings have essentially, if not exactly, the same type of barbule as is to be noted in the corresponding adult, it follows that the feathers of the latter are nothing more than simple or specialised down barbules.

Strange, therefore, as it may appear, *all* the feathers borne by the adult Ostrich or by any other struthious form, whether they are situated on the wing, tail, or body generally, are nothing more than down, or modified down.

There is not the slightest evidence of a teleoptylic phase of feathering comparable to that seen in the carinate flying bird, so that to regard the struthious wing-feather as secondarily derived from a proto-carinate volant feather, or in any way as a degenerate structure, seems to me completely unjustified by the evidence.

Duerden (1920, p. 626) takes the view that *filoplumes* are degenerate pennæ. As the general opinion of all authorities who have studied the pterylosis of the Struthiones is that filoplumes are not to be found in this group, this would seem to explain their absence, since, as we have endeavoured to prove above, pennaceous pennæ or teleoptiles are completely unrepresented in this group.

THE AFTERSHAFT.

The conspicuous aftershafts in the adult Emu and Cassowary are too well known to need description here. Aftershafts are also present in the young of both these birds. In *Struthio* and *Rhea* they are not present, at any rate in the adult *Struthio*, although I believe there is good reason to suppose that there are signs of their presence in the chick of this last bird (see also below, p. 208). Apparently the presence of a not very conspicuous aftershaft in the chicks of the Emu and Cassowary led to the almost universal acceptance of the opinion that the aftershaft is not a primitive feature, but has been secondarily acquired in all birds.

Professor Cossar Ewart (1921), however, in an extremely interesting and very illuminating paper on "The Nestling Feathers of the Mallard, with Observations on the Composition, Origin and History of Feathers," has, I think, conclusively demonstrated that the aftershaft is a primitive feature. He says (p. 627):—"The chief reasons given for regarding the aftershaft as an accessory and secondarily acquired structure are (1) that the aftershaft is developed from a forward elongation of the calamus, and (2) that the tip of the aftershaft of the new feather is never attached to the calamus of the feather about to be shed—that, for example, in the Emu the tip of the aftershaft of the feather of the second generation is from first to last free."

"If," he goes on to say, "I succeed in showing that the aftershaft, like the shaft, grows from apex to base and is completed before the calamus is formed, and that, during development, the tip of the aftershaft is connected with the calamus of the feather about to be shed—is, in other words, for a time attached to the old feather—it may safely be assumed that the aftershaft is a primitive feature, and that a complete true feather (penna), like a down feather (plumula), consists of two shafts or blades." In point of fact, Cossar Ewart not only proves this, as I think everyone who reads his paper will agree, but he demonstrates that the protoptile of the Emu, which has been often assumed to have "no distinct aftershaft," not only has a very definite one, but that the two following generations of feathers are provided with aftershafts as well, and that they are developmentally in continuity one with the other (*cf.* text-fig. 11, p. 622, *l. c.*).

The facts brought forward by Cossar Ewart in connection with the developmental history of the aftershaft are extremely interesting as bearing on the generally admitted view that the Emu and Cassowary are more primitve in their characters than the more specialised Rhea and Ostrich, while as regards the old view of the secondary nature of the aftershaft, it has once more been shown how apparently perverse have been the views held in regard to so many of the characters of the Palæognathæ.

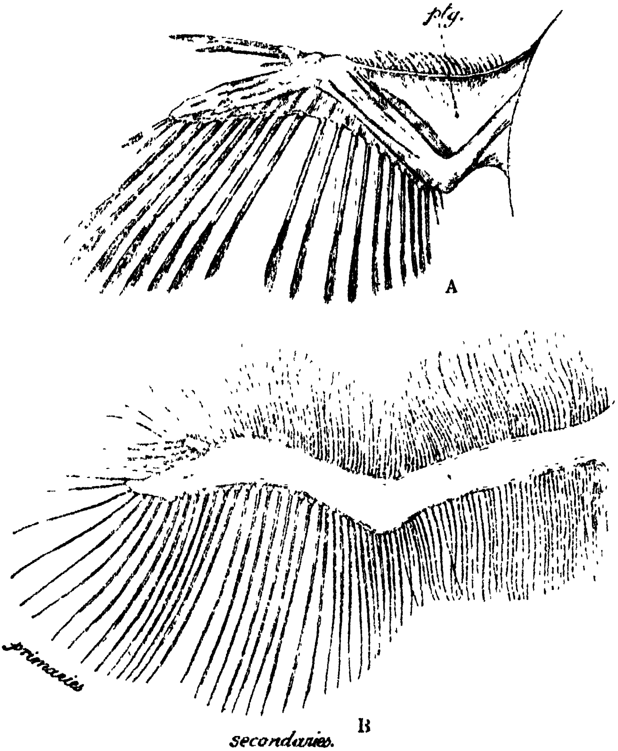
I might add that in the Tinamous the aftershaft in the chick is as long as the main shaft, while in the adult it is very short or hardly visible, a condition which, in view of the fact that Tinamous fly, may possibly be regarded as secondary.

In the Tinamou chick the distal ends of the aftershafts of the dorsal feathers have a clumped arrangement and a silvery or paper-like appearance, the result being that an effect is produced which closely approximates to the long papery spear-like shafts seen in the protoptiles on the dorsum of the Ostrich chick. This latter curious modification in the Ostrich chick is, so far as I am aware, unique in the protoptiles of the chicks of other birds, and from their rather isolated disposition as regards the rest of the protoptile, which has an umbelliform structure, I make the suggestion here that they may be specialised aftershafts.

THE QUESTION OF THE PATAGIUM.

Jeffery Parker (1892), in his well-known paper on the anatomy and development of *Apteryx*, says:—Another fact which appears to me to tell in favour of the derivation of *Apteryx* from a progenitor with well-developed wings is the fact that the wing is provided with a true alar membrane." Pycraft, as I have previously mentioned, quoted this as an important and convincing piece of evidence in favour of Parker's supposition and as if it applied in a general way to the Palæognathæ (cf. *l. c.* p. 260).

Text figure 9.



A. Fore-limb of nestling Yellow-Hammer (*Emberiza citrinella*), inner view, to show patagium (*ptg.*). About natural size.

B. Fore-limb of embryo *Rhea pennata*, inner view, to show absence of patagium. Natural size.

I have examined the fore-limb of a specimen of *Apteryx oweni*, which has been preserved in spirit in the British Museum and which, moreover, was in an excellent state of preservation, and it exhibits such negative evidence of a pre- or post-patagium that if it had not been for Parker's statement that the wing of a perfectly fresh specimen of *Apteryx bulleri* was shown in figs. 14 & 15 (pl. 3) of his paper, it would never have occurred to me for a moment that a patagium might be present in the specimen which I have examined. I should have said that there was a certain laxity of skin which was a matter of necessity in situations where movement of such a structure as the avian fore-limb was constantly taking place. This is borne out by Owen, who, as long ago as 1840, called attention to the fact that "the antibrachium is retained in a state of permanent flexion by the surrounding integument of the wing; and it cannot be brought by forcible extension beyond an angle of 45° with the humerus." I could find, moreover, no trace whatever of patagia in other embryos of *Apteryx* similarly preserved in spirit, and not only this, but not a trace in the embryos of *Struthio*, *Rhea*, *Casuarius*, or *Dromæus*, or, for that matter, in any adult examples.

The figure of a fore-limb of an embryo Rhea (B.M. 1925.4.10. 29.31), presented by Colonel Morley Knight, and taken from the egg by myself, is shown in text-fig. 9 B, and attention is not only drawn to the complete absence of patagia, but to the interesting row of closely opposed feathers which are, along the pre-axial border of the arm (humerus), nearly as well developed as the primaries or secondaries (see also Pl. I.). This absence of any indication of a patagium in the embryos of the Struthiones mentioned is a most important piece of evidence, all the more so because the patagia in the embryos of flying birds (as for example, that of the Yellow Hammer, text-fig. 9 A) are so conspicuous. It seems to me to indicate the very opposite conclusion which Parker drew and Pycraft adopted.

THE FORE-LIMB.

Degeneration or retrogression in the fore-limb of the Struthiones is, in some respects, an obvious fact which it would be idle to deny, although in some cases it seems difficult to distinguish between retrogression and specialisation. In any case, neither retrogression nor even complete loss of the wing appears to me to be any bar to the acceptance of the view that the ancestors of this primitive group of birds were not descended from a volant stock, and that their present-day survivors represent direct line relics of an ancient avifauna which marked an early stage in the evolution of the bird from some Proto-Pseudosuchian ancestor.

Flight at this early stage had presumably not as yet been attained, and the view taken here is that the struthious wing, in as far as it is either retrocedent or specialised, represents a retrogression or a specialisation from the primitive generalised and non-volant sauropsidan fore-limb. This point will be taken up again in greater detail in the case of the wing of *Apteryx* and *Casuarius*. In the meanwhile it would also seem to follow as a corollary from the above view that the primitive bird was cursorial, and that a considerable time must have elapsed before the primary feather coat, originally in all probability a uniform "pelage," had been sufficiently specialised in the appropriate places to admit even of the possibility of or potentiality for flight.* It may be further added that the primitive feather and its feather papillæ, as recently pointed out by Professor Cossar Ewart (1921), was probably evolved in close association with, but quite independently of, the scales which have been considered to have covered the body of the primitive bird ancestor, while there does not appear to be the least reason to suspect that the view so often expressed, that the original feather was a secondary modification of the scale, has any basis in fact or of probability.

The complete disappearance of the fore-limb in some forms such as the Moas, or its partial disappearance in others as the Emus or Kiwis, has been suggested as an obstacle to the ideas expressed above, since it has almost invariably been held that this disappearance or retrogression marks the end of a degenerate course from a flying to a flightless phase. It is not denied that this retrogression may in some groups be a degenerate phenomenon, although the wings of the Ostrich and Rhea are regarded here as representing the probable high-water mark of specialisation towards flight reached by the Palæognathous group as a whole (see p. 201). It even seems possible, for instance, that these retrocedent wings in certain struthious groups were the secondary result of local conditions to be alluded to presently, and in some cases may even have been of comparatively recent origin ; but the idea which is put forward here is that the primitive bird groups in the early days of their evolution, although possessing feathered fore-limbs, only possessed "wings" in an early stage of development in which the feather itself had not advanced beyond a prepennal down-like phase, and that in some basal groups the evolution of these "wings" never advanced far enough to become anything more than pseudo-wings, a failure of development which may have been due to causes outside the wing itself, as, for instance, a failure to evolve specialised muscle-groups connected with the sternum, or special ossifying centres in that structure, or to other physiological or germinal causes.

It should, moreover, be remembered that in certain Theropodous Dinosaurs (*Anchisaurus*, *Ceratosaurus*, *Tyrannosaurus*) we can trace a progressive diminution of the fore-limb through successive geological horizons, while in *Gorgosaurus* retrogression seems, in comparison with the huge bulk of this animal, to have reached a point which verges almost on the ridiculous and is only comparable in degree with what may have occurred in the Moas. This retrogression or specialisation in the Dinosaurs, it seems needless to remark, occurred independently of any question of flight. What therefore happened in the case of the Theropodous Dinosaurs and Cœlurosaurs might well have been reflected in some of the primitive cursorial birds, and either have been the cause of, or the result of, that cursorial mode of life.

---

* Owing to considerations of space I have endeavoured, in so far as is possible, to avoid involving myself here in a discussion on the origin of flight, and for this reason Baron Nopcsa's theories and others are not discussed.

In the bipedal swiftly-running Cœlurosaurs (*e.g.*, *Compsognathus*, *Procompsognathus*, *Saltopus*, and *Struthiomimus*) it will now be generally admitted, as the result of the work of Osborn, Watson, Broom, von Huene, and others, that there was an obvious tendency to a development parallel with and, as regards skeletal features, amazingly similar to what must have simultaneously existed in the primitive bird.

Archæopteryx, too, although apparently a long way from being on the direct avian line, was, from what we know of its skeletal characters, certainly a "reptilian bird," or more reptile than bird, just as *Struthiomimus*, although developed for a different mode of life, might almost be termed an "avian reptile." It is not difficult to imagine that the Palæognathous ancestor was very similar in appearance and habits to some such form as *Struthiomimus*.

Broom (1913, p. 630 *et seq.*), in a paper on the South African *Pseudosuchia*, discusses the ancestral relations which he considers to have existed between this group of primitive reptiles and the Theropodous Dinosaurs on the one hand and birds on the other. "In those points," he says, "where we find the Dinosaurs," and we may now I think add the Cœlurosaurs, "too specialised," to have given rise to the avian ancestor, "we find the Pseudosuchian still primitive enough."

Living side by side, therefore, in Cretaceous days we might have found such a reptile as the Ostrich-like Cœlurosaur—*Struthiomimus*—and the struthious desert-running ancestor. It seems conceivable that only the zoological expert could have differentiated between the Jurassic or Triassic ancestors of these two creatures, fundamentally different as they really were. Yet the "wing" of the bird with its scale-protected downy protoptyles had a *potential* power to specialise in the direction of the perfect avian wing with its full volant armature.

In the struthious phylum, for one reason or another, this goal was apparently never fully attained. As regards feather structure, evolution in their case never seems to have reached a higher or more specialised level than a simple or modified pre-pennal down. There is no evidence to suggest that the pennal phase was ever reached.

As has been mentioned above, the wings of the Ostrich and Rhea possibly represent the extreme limit attained in the Struthiones towards a truly volant structure. In this division it would appear that the wing never seems to have been more than a balancing agent and an extra aid to speed in running. In virtue of the fact that the Ostrich is even now continually *attempting* to use its wings there seems to be no valid reason to explain why it should ever have lost the priceless gift of flight, presuming that it originally possessed such a gift.

But poor as was the standard of "flight" attained by the

Ostrich and Rhea they apparently succeeded in maintaining it in virtue of the fact that there was always in their case the incentive of open wide-spreading veldts, pampas, and deserts, or the ever-present danger of carnivorous foes throughout the Tertiary. As regards the rest of the existing Struthiones the Emus of the present day are birds of dry open forest, the Cassowaries of dense humid undergrowth, while the Kiwis, in addition to being nocturnal, inhabit deep and dark gullies or thick scrub, where in the daytime they live almost a subterranean existence.

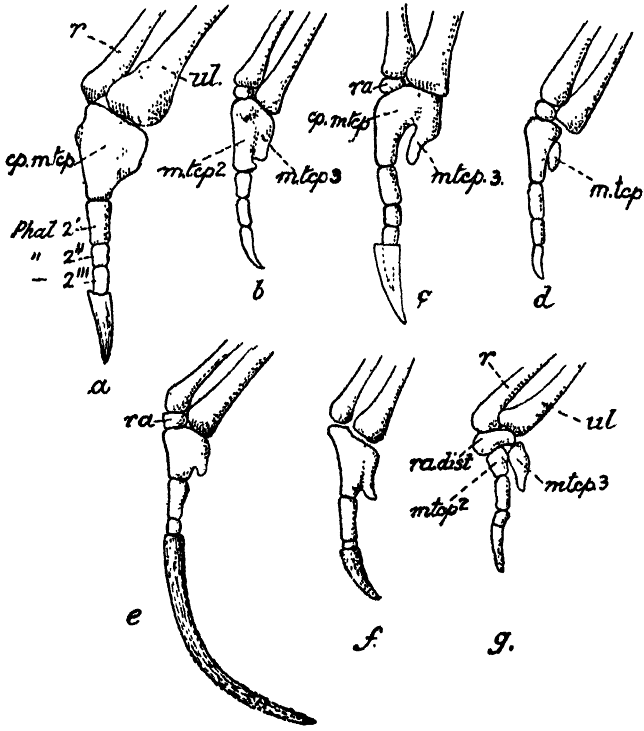
Insulation may have saved the Cassowary and Emu from the carnivora of the Eurasian continents, just as it saved *Æpyornis* in Madagascar or the Moa in ancient New Zealand (Antipodea).

But whatever degree of specialisation of the fore-limb comparable to that of the Ostrich or Rhea, the Cassowary, Emu, or Kiwi may or may not have formerly attained in the direction of a pseudo-volant lifting power of the wing, combined with cursorial speed, it seems at any rate likely that insulation and local conditions would have exacted their penalty. Thus, from this point of view, it might be held that the conditions to which these last birds were exposed in the later stages of their history, whether they took the form of extreme afforestation, insulation, or freedom from predatory foes, would not have provided either the scope or the stimulus which would have been necessary to maintain whatever standard of efficiency of the wing they might have attained. Poor as this standard might have been, even that which they had attained would have been taken from them.

From what we know, however, of the developmental and osteological conditions obtaining in the forearm and manus of *Apteryx* (Parker, 1892, p. 93, pl. 17), it seems to me very doubtful if in the case of this form, at any rate, the wing ever attained even to the standard of utility possessed by the Ostrich or Rhea. Parker, for instance, figures (1882, pl. 17, fig. 247) the metacarpals of *A. bulleri*, among several others, and says: "It is worth noticing this is probably the only recorded example of a fully adult recent bird with free metacarpals." In another adult example, removed from a skin, he records that the third metacarpal was free. In an embryo of *Apteryx australis* the same authority found not only a separate *radiale ulnare* and distal carpal mass, but also an *intermedium*, an element which has so far only been found in *Opisthocomus*, an extremely primitive form and a notoriously very feeble flier. It also seems difficult to examine the figures of the manus of various species of *Apteryx* which Parker gives (pl. 17, figs. 241–253) without coming to the conclusion that we are faced with a relatively primitive and unspecialised morphological status, or at least one which it seems difficult to reconcile with a secondary degenerative process following a fully volant condition. We seem to have under observation specialised bony changes of the primitive manus which would appear to be consequent upon a condition of primary flightlessness in a primarily cursorial bird. Had they been secondary to a prevolant condition it is difficult, for instance, to see how we could have such a condition as the free metacarpal in the adult *Apteryx bulleri* just referred to (*cf.* text-fig. 10 *g*).

It may well be, therefore, that in *Apteryx*, as also in *Dromæus* and *Casuarius*, the osteological features of the fore-arm rather indicate a modified condition of the primitive flightless wing than a degenerate phase of a wing which had once functioned as a piece of volant mechanism. In the fore-limb of the Ostrich and the Rhea we get evidence of the same primitive and relatively unspecialised phase (*cf.* p. 229 and text-figs. 19, 20, and 21).

Text-figure 10.

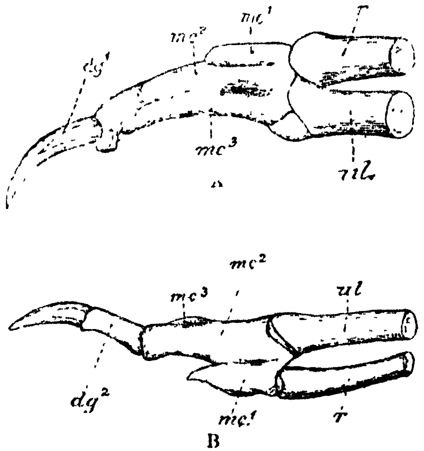


Metacarpals in the hand of various species of adult *Apteryx*, after Jeffery Parker, showing a condition difficult to reconcile with a previous volant phase: compare, for example, the free metacarpal in *g*.

Emphasis may also be laid here on the fact that all the arguments, anatomical and otherwise, which are brought forward in this paper in support of the view that the ancestral Struthiones were from the first non-fliers apply with special force to *Apteryx*. For, if it were true that the disproportion between the wings and hinder extremities in that form had followed as a result of the loss of flight, with a concomitant increase in size and bulk of the body, the Kiwis must have been originally so small as to make the loss of flight wholly inexplicable. In *Apteryx*, too, the structure of the remiges is not only more down-like than usual, but is exactly what we might expect in a primitive remex, for the calamus and rachis are exceptionally well developed, the barbs are very numerous, and the barbules in an early down stage of development.

Again, I do not think it could be denied that the fore-limb of the Cassowary, in addition to the obvious degradation in size which it has undergone, shows a good deal of specialisation. If, for instance, the remex of an unhatched embryo of *Casuarius* be compared with a greater wing-covert of the same embryo, it seems to me pretty clear that the condition of the remex is *not a degenerate phase of a teleoptylic volant feather*, but a specialisation of the pre-pennal down-like phase, so that in the remex of the young *Apteryx*, and in the wing-coverts and the remex of the embryo Cassowary we can trace successive stages from the primitive condition to the highly modified spiny wing-quills of the adult Cassowary. The importance of this, if my contention is correct, hardly needs to be emphasised.

Text-figure 11.



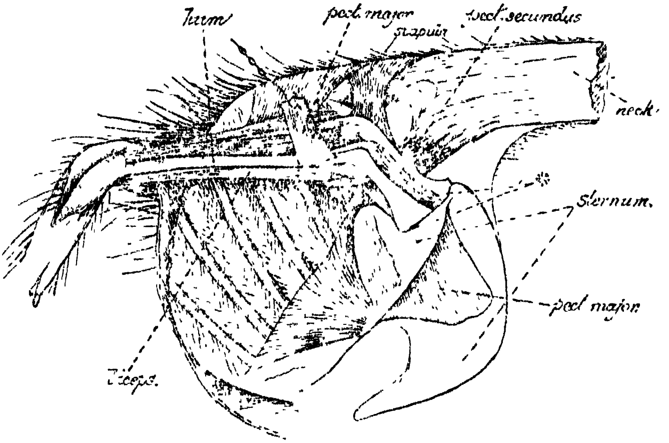
Metacarpals in the hand of an adult *Casuarius* (A), and an adult *Apteryx oweni* (B); after Kitchin Parker.

It is not possible in a paper like the present to discuss the anatomy of the struthious fore-limb as freely as it deserves, but before leaving the subject I should like to note briefly a few points of interest connected with its myology which have come to light during my investigations.

Beddard (1898, p. 501) puts the total number of muscles in the hand of the Ostrich as twenty-three. He says: "It appears, therefore, that in spite of the small size of the manus of the Ostrich relatively to that of flying birds, there is but little evidence of degeneration in its musculature. On the contrary, indeed, for it might be said that the wing muscles of *Struthio* are less degenerate, or at any rate less modified, than those of carinates, in that the amount of muscle as compared with tendon is greater. The complication of the conjoined flexores digitorum is highly suggestive of a walking or climbing animal. It seems to be conceivable that the Ostrich branched off from the avian stem before the power of flight was perfectly established."

To this I may here add that there seems enough anatomical evidence to justify the hypothesis that the Tinamous left this avian stem subsequently to the Struthiones on a side line of their own, but still before flight in its fully perfect condition had been attained. They are "Palæognathous" or primitive, that is to say, in all points except those intimately concerned with the function of flight.

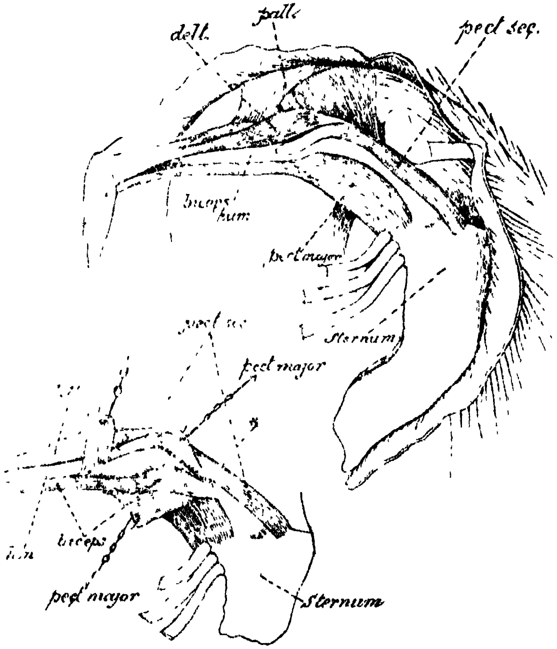
Text-figure 12.



Dissection of pectoral muscles in ostrich embryo.

It seems a little unfortunate, therefore, that Beddard (*loc. cit.* p. 498), in giving a summary of the musculature of all the struthious genera, should have stated that the following muscles have disappeared: *Pectoralis propatagialis*, *Biceps propatagialis*, *Deltoides propatagialis*, *Deltoides minor*, *Scapulo-humeralis anterior*, and *Expansor secundariorum*, while the *Pectoralis major* is in all "very reduced," for since, as I have already pointed out, there is no sign or hint of a patagium in any of the struthious embryos or adults, it would appear to be more likely that these patagial and accessory flying muscles were never developed. Moreover, the *Expansor secundariorum*, so far at any rate as the Rhea is concerned, has by no means disappeared (*see* p. 221). Again, as regards the so-called reduction of the *Pectoralis major*, it seems to me at least a very open question whether the anatomical features presented by this muscle and the other pectorals in *Struthio* and *Rhea* are not evidence of a primitive phase of development rather than a degenerate condition. I have made careful dissections of these muscles in

Text-figure 13.



Dissection of pectoral muscles of embryo *Rhea* to show the apparently composite nature of *Pectoralis major* and biceps muscles; *cf.* text.

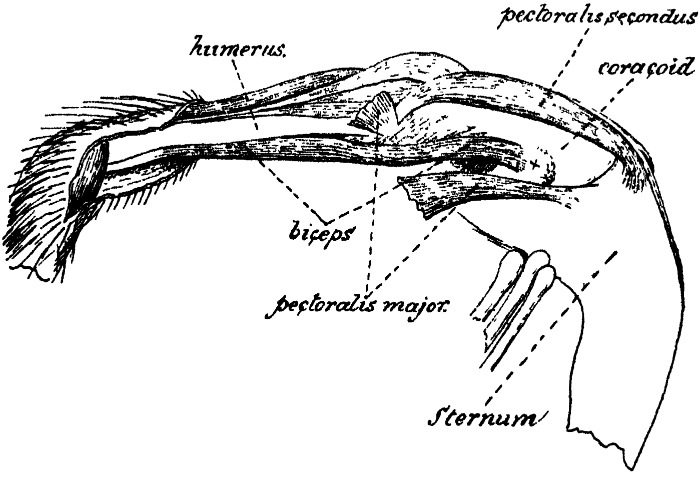
the just unhatched embryos of both these forms, and figures are given of them (text-figs. 12 and 13).

It will be noticed, for instance, that in the Rhea the *Pectoralis major* has no sternal origin at all, but derives its origin from the outer face of the posterior part of the coracoid. Converging outwards and upwards to its humeral attachment on the pectoral ridge, it first blends with the *Pectoralis tertius*, which takes origin from the costal process of the sternum, and becomes so intimately involved with it and the biceps muscle, which is almost completely surrounded in part of its course, that on a first exposure of these three muscles the impression gained is that of a single composite muscle (*cf.* text-fig. 13).

It requires, in fact, a little care to demonstrate the identity of the individual components of this group.

Furthermore, on cutting through the pectoral the biceps is seen to arise in a very anomalous position, viz., far back on the outer margin of the coracoid, that is to say, from almost *the sternal end* of that bone (*cf.* text-fig. 14), and therefore far removed from its head or scapula end, which is the usual seat of origin for the coracoidal head of the biceps in modern birds. There is, moreover, no indication whatever of a humeral head. This origin of the biceps in *Rhea* is especially interesting in view of the fact that Owen (1866, iii. p. 6), in describing the muscle in the *Monotremata*, records that both heads are coracoidal in origin and that one of them (the long head) arises from the *sternal end* of the coracoid, while Günther (1868) states that in *Hatteria* the inner or long head of the same muscle also arises from the "sternal margin" of that bone. I have been at some pains to dissect and illustrate these muscles because degeneration following upon loss of flight does not seem in the least adequate to explain the problem of their morphology; while, on the other hand, their study seems to indicate, beyond little room for doubt, that we are dealing here with a primitive phase in the evolution of avian muscles.

Text-figure 14.



Dissection of biceps muscle in embryo *Rhea* to show origin of long head from coracoidal spine *; *cf.* text.

A still more interesting feature is connected with the morphology of the *Pectoralis secundus* muscle in *Rhea*, *Struthio*, and

Apteryx, and I am constrained to think that the anatomy of this muscle may have been a factor which largely contributed to the failure to attain to flight not only in these but possibly in other primitive birds.

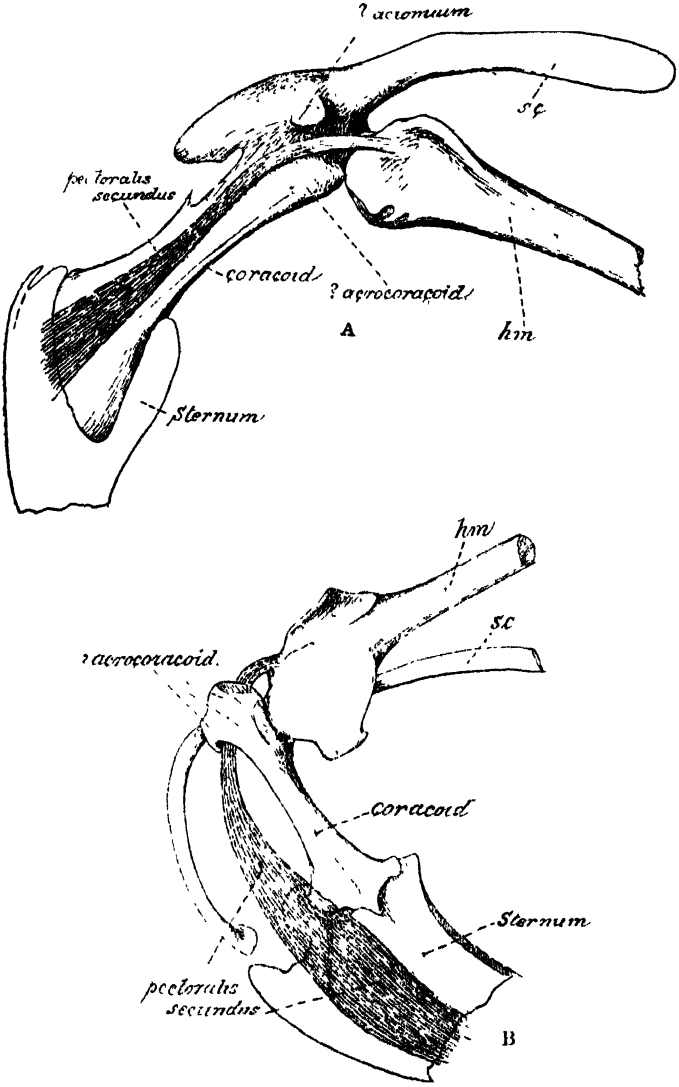
In carinate birds and in the Tinamous the fibres of this large and important elevator of the wing converge from their spacious origin on the sternum to form a rounded tendinous cord, which passes upwards and outwards to the *inner and posterior aspect* of the head of the coracoid. This tendon then passes through the foramen triosseum, and on its exit is sharply deflected almost at right angles in its course to its ultimate attachment to the head of the humerus, the foramen acting as a strong pulley in the raising of the fore-limb (*cf.* text-fig. 15 B).

In the Rhea, Ostrich, and *Apteryx*, on the other hand, it would appear to have been overlooked that the semi-tendinous cord of insertion not only does not pass through a foramen triosseum (which does not exist), but that it merely passes along a shallow groove on the *outer and anterior surface* of the head of the coracoid (*cf.* text-fig. 15 A). Thus, at first sight, it would appear as if the tendons in the two categories under notice took different courses. In reality this is not so, for whereas in the flying bird the tendon passes round the inner side of the very prominent acrocoracoidal process of the distal end of the coracoid, in the struthious bird this acrocoracoid does not exist, or at the most only exists as a rudimentary beginning represented by a slight bony eminence or ridge of bone (*cf.* text-fig. 15 A). The tendon passes to the inner side of this low eminence on the coracoid, lying between it and a prominent boss of bone (? the acromium) on the scapula. If the rudiment of the acrocoracoid had developed it would have grown in a forward and inward direction over the tendon so as to have furnished the same sort of pulley or fulcrum as that round which the tendon in flying birds plays.

It is obvious, therefore, that in the Struthiones, or at any rate in those forms mentioned above, the *pectoralis secundus* muscle can only derive the most feeble and precarious leverage from this rudiment for its elevating action on the humerus. It may, of course, be argued that the rudiment in question is not in reality an incipient indication of the acrocoracoid but a relic of it secondary to a loss of flight. In view of the evidence afforded, however, by so many other structural features in the Struthiones the view taken here is that it is a true rudimentary acrocoracoid. This view, at any rate, is supported by the fact that in *Didus*, *Aptornis*, and other flightless forms, the acrocoracoid is especially well developed and shows little if any signs of degeneration.

It is evident, however, that Jeffery Parker (1892) in his observations on the development of *Apteryx* (p. 91) takes an opposite view, for in certain stages of growth (F. & G., pl. 17, figs. 234–236) he calls attention to the increased development of the acrocoracoidal tuberosity, "which is now a well-marked

Text-figure 15.

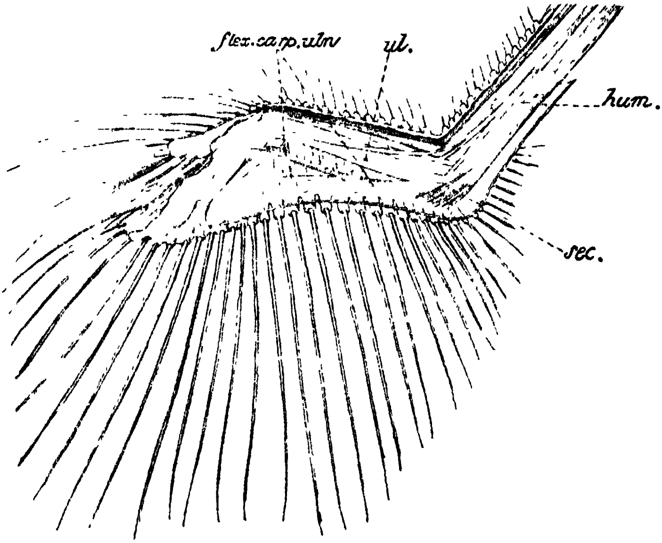


Dissection of *Pectoralis secundus* muscles in A. Rhea and B. Skua; *cf.* text.

process considerably larger proportionately than in the adult." When, however, we examine these plates this so-called tuberosity seems to be nothing more than a low oval-shaped and ill-defined concrescence. It is a featureless structure or nodule which seems to me to do little more than mark the site of a still-born acrocoracoid. At the stages of growth of the shoulder-girdle depicted by Parker the various topographical features, such as the glenoid cavity, procoracoid, and coracoidal foramen, are well defined. The acrocoracoid alone lags behind, just as it does in the adult, and the only explanation to my mind is that it is "still-born."

I may also add that, although I have only dissected the *pectoralis secundus* muscle in the struthious forms specifically mentioned above, as well as a good many carinate forms, it seems quite clear from the comparative morphology of the bony parts concerned that the muscle was similarly handicapped in such forms as the Emu and Cassowary and even in the Moas and *Diatryma*.

Text figure 16.

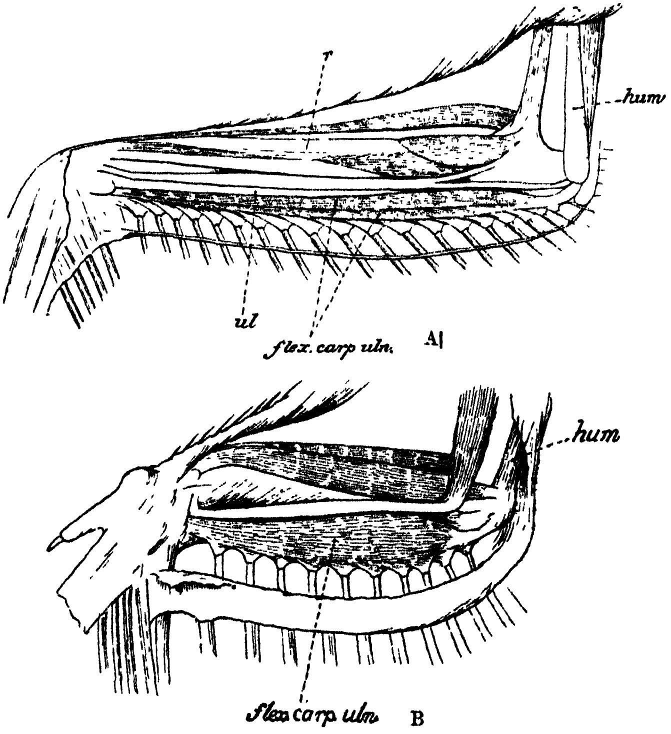


Dissection of *Flexor carpi ulnaris* muscle in embryo Rhea to show bipartite condition; *cf.* text.

The *pectoralis secundus*, as has been pointed out by Shufeldt (1890, p. 73) in the case of the Raven and by Kitchin Parker (1864, p. 229) in the case of the Tinamou, through the leverage gained by its tendon passing through the osseous canal formed by the bones of the shoulder-girdle (coracoid, scapula, and clavicle), acts as a strong elevator of the humerus and plays a most important and fundamental part in the function of flight; while, as I have suggested above, it seems difficult to resist the conclusion that the peculiar conditions in the three struthious birds mentioned, with a consequent loss of leverage, may have played a very important part in the failure to attain to flight in not only these birds but in other primitive forms.

The *Flexor carpi ulnaris* is another muscle worthy of a moment's consideration. There seems to be little doubt that, as suggested by Shufeldt (*loc. cit.* p. 144), this muscle was originally composed of two parts, or perhaps two distinct muscles. This is indicated in the Raven, and I may add many other birds, by the median fascia that runs longitudinally through its belly. I have exposed this muscle in the just-hatched embryo *Rhea*, and the original bipartite condition is beautifully shown in text-fig. 16. I do not think that further words are necessary to emphasise the lesson which can be drawn from it. It only remains to add that in the Tinamou (*cf.* text-fig. 17 B) we have a phase of development of this muscle which is far in advance of the Palæognathous but has not quite attained to the fully-developed carinate or Neognathous stage.

Text-figure 17.



Dissection of *Flexor carpi ulnaris* muscle in A. *Œdicnemus* and B. Tinamou (*Nothura maculosa*); *cf.* text. Natural size.

Finally, it may be said that in most flying birds that extraordinarily little muscle known as the *Expansor secundariorum* is seen to be attached to not more than the innermost two or three inner secondary feathers. In the *Rhea* embryo (see text-fig. 16) I have found that it is attached to the six innermost. Here again, therefore, we seem far from having evidence of a state of things pointing to degeneration, but, on the contrary, indications of a primitive condition pointing to a time when this muscle may have played a more important part than it does now.

THE CORACO-SCAPULAR BAR.

In the Struthiones, as also in some primitive and fossil types of flightless birds such as the Eocene *Diatryma* (Mathew & Granger, 1917), the scapular and coracoid are fused together into a continuous and uninterrupted bar of bone, while instead of being inclined at a pronounced angle they hold an end-on position, one to the other, so that they lie in almost the same straight line and the same plane.

In the Neognathæ, or what may be called modern flying and carinate birds, the angle made by the two bones is, on the contrary, generally less than a right angle, and they do not lie in anything like the same plane. In addition, there is a marked solution of continuity where the two make contact which almost amounts to a joint.

Moreover, in such struthious forms where the wings have *not* apparently undergone a secondary retrogression in any respect except that of size or proportion, such as the Ostrich and Rhea, the coracoid is a short flattened structure with a quadrilateral form strongly contrasted with the elongated and somewhat rod- or strut-shaped structure characteristic of the flying Neognathine bird. There are other obvious points of difference which need not detain us, since all I wish to emphasise here is, that if we go back to such primitive reptilian forms as *Euparkeria* and *Ornithosuchus*, we find in the coracoid and scapula of these representatives of the Pseudosuchian group of reptiles a most remarkable similarity to the Palæognathus coraco-scapular bar as regards their fusion, form, and end-on position, to say nothing of other points, such as the position and presence of the coracoidal foramen. This similarity is so remarkable that it can hardly fail to suggest some more or less close phylogenetic relationship. The same morphological similarity can be traced in the coraco-scapular bar of various Lizards by studying the abundant series of illustrations in such a work as Kitchin Parker's on the vertebrate shoulder-joint.

The Pseudosuchian reptiles alluded to above, it may be recalled, are now regarded by the latest authorities as being probably derived from an ancestral type which gave rise to birds and such Dinosaurian forms as the Cœlurosaurs and Theropoda.

In this remarkable similarity then there seems to be justifiable ground for, at any rate, a preliminary assumption that the morphology of the coraco-scapular bar in the Struthiones is reptilian or primary, and not secondary to a loss of flight as has been so often maintained.

On the other hand, in the relations of the coraco-scapular bar obtaining in the Neognathæ, we seem justified in assuming a condition which has been acquired as the result, among other factors, of the development of flying muscles, a condition which is presumably secondary.

When, too, we reflect that present existing, as well as fossil Palæognathæ, exhibit a mass of primitive characters which can only be expressive of an early stage of avian evolution and which, as it seems to me, must on no account be confounded with degenerative or retrogressive processes, the assumption which we have permitted ourselves seems all the more justified.

Opposite opinions, however, have been generally, if not universally, held.

T. J. Parker (1882) for instance, in a paper on *Notornis* and other flightless birds, was especially prominent in arguing that there was no morphological gap in the two categories alluded to, while in some general remarks on flightless birds he considers the "Ratitæ" (p. 255) as the greatly specialised but degenerate descendants of "Carinate" birds. In a paper, too, on the Anatomy and Development of *Apteryx* (1892), he has given a number of characters which, if we are to follow him and Pycraft (1898), lend the strongest support to the view that the Struthiones must be descendants of a proto-carinate avian form capable of flight.

There are, of course, many morphological facts connected with the problem of flight in birds which are both interesting and apparently contradictory. These problems, however, I do not propose to discuss here, as it is my immediate intention to discuss the comparative anatomy of the Struthious and reptilian shoulder-girdle as revealed by the conditions met with in the embryo. Before doing so, however, I might mention that Parker (*l. c.* p. 250) writes that "it would, however, be a mistake to suppose that there is anything like a constant relation between flightlessness and increase of the coraco-scapular angle." For instance, he calls attention to the fact that in one of the best fliers in the avian class, that is to say in the Albatross, the angle subtended by the scapula and coracoid is 100° or greater than in any other flying bird.

On the other hand, it is interesting to note that in *Stringops*, the flightless Owl-Parrot of New Zealand, the coraco-scapular angle has undergone little or no increase in a bird in which the carina or keel is practically non-existent. This, of course, might very easily be ascribed to the possible fact that the loss of flight may have been comparatively recent, notwithstanding the disappearance of the keel; but against this seem to be the primitive features of the skull, while it may be stated that

Dr. H. O. Forbes (1893, p. 544) has recorded that a Mr. Shand and an aged Moriori called "Tapu" informed him that the Kakapo (*Stringops*) occupied in the early days of the settlement of Wharekauri, the largest of the Chatham Islands, "various parts of the island in considerable numbers, and both remember their burrows," though Mr. Shand could not recall having himself seen the birds. If the statements made to Dr. Forbes were true it would relegate the flightless condition of this primitive Parrot to an immense antiquity, for obvious reasons which we need not stop to discuss.

Again, it is generally held, and no doubt with a good deal of truth, that the lengthening of the coracoid is correlated with the ability to fly, in order, as it is said, to accommodate a large pectoral muscle; but I have recently called attention (1924) to the fact that the very peculiar and generalised flightless bird *Mesites* of Madagascar is provided with a coracoid which, relatively to its sternum, is the longest coracoid I have ever seen, with the exception, perhaps, of the flightless Rail *Atlantisia rogersi* of Inaccessible Island (1928). In addition to the long coracoid *Mesites* has well-developed pectorals, a very reduced keel, not a vestige of a clavicle, and an extremely reduced coraco-scapular angle—to be concise 58°.

That *Mesites* is, to say the least, to a very large extent dependent on its cursorial powers is evident from its very well-developed hind limbs and a pelvis which has been specialised on almost the exact lines of the Californian Road-Runner (*Geococcyx mexicana*).

Leaving, however, such contradictory instances of the conditions generally accepted as characteristic of the volant state and coming at once to a consideration of the relations of the coracoid and scapula to one another in the embryo of the Ostrich, we find that Miss Lindsay (1885), in her now classical and still almost unique paper on the sternum in the Avian embryo, describes the scapula and coracoid in the four-days Ostrich embryo *as not being united*! In the five-days (Galline) chick, too, the scapula and coracoid are stated to be first perfectly distinct, then as becoming fused, and, finally, as being once again separate in the older chick. This temporary fusion, Beddard thought, might be significant of the struthionic condition, and it is to be noted that Miss Lindsay came to the conclusion that the "subsequent" union of the coracoid and scapula in the Ostrich is a secondary rather than an ancestral reptilian condition.

On the other hand, no trace was found by Miss Lindsay of either interclavicle, clavicle, or keel, and the suggestion that the sternum of the Ratitæ has lost a formerly-existing keel "must now be directly negatived." These results of Miss Lindsay's researches, I may add, were obtained by dissection!

Broom (1906, p. 357), in a paper "On the Early Development of the Appendicular Skeleton of the Ostrich," in discussing Miss Lindsay's results, also doubts the possibility of being able to dissect out the elements of the shoulder-girdle in the chick at a stage when sections "show comparatively little differentiation in the cells," and he feels "considerable hesitation in believing in structures which can be got by dissection but cannot be seen in microscopic sections." In fact, he found in the ten-days' embryo Ostrich, in contradistinction to Miss Lindsay's results, "no trace of a division between the coracoid and scapula; both are merely parts of a single bar." Incidentally, he finds the coracoid to be a short broad structure (as in the adult), and that there is no clavicle present.

Broom's studies were carried out by tangential and transverse sections twenty-one years after Miss Lindsay's work, so that, allowing for improved methods of investigation, one may feel satisfied that in his description we have revealed the true facts in regard to the one-ness of the coraco-scapular bar in the early struthious embryo.

When, too, we bear in mind the almost identical morphological picture which obtains in such primitive reptilian types as *Euparkeria*, *Ornithosuchus*, and others, it seems difficult to resist the conclusion that the condition is a primary reptilian-derived condition, and not only so in the Ostrich but in the rest of the Palæognathæ, not to mention such other primitive avian and flightless types as *Diatryma*, in which we also get a similar fusion of these two bones, the same end-on relations in the scapula and coracoid, and the same flattened, short, and quadrilateral form of the latter bone.

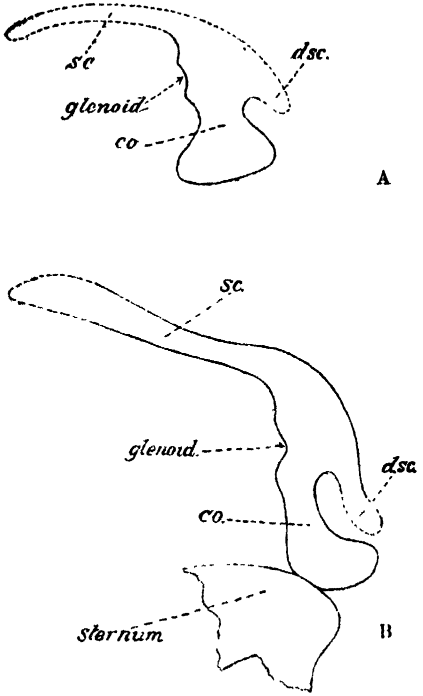
Broom, however, states (*l. c.* p. 357) that in the ten-days' old Ostrich embryo the long axis of the scapula makes an angle of about 100° with that of the coracoid, but that by the next day it has become more obtuse. In the figures given by Broom (*cf.* text-fig. 18) the condition present seems to me more of a gradual bend than an angle, and in any case the absolute unity of the coraco-scapular complex seems to be the over-ruling and most important point.

Nevertheless, Broom sees evidence of a flying ancestor in this inclination of the two structures to one another. Thus he goes on to say:—"When the ancestor of the Ostrich became a flying bird the coracoid would become elongated to accommodate a large pectoral muscle and there would doubtless be a large clavicle. The ten-days' embryo still shows evidence of the flying ancestor in the well-marked angle which there is between the scapula and coracoid. As the power of flight became lost the clavicle disappeared."

In other words, if I have interpreted his conclusions correctly, Broom is of the opinion that the end-on fused condition of the coraco-scapular bar in the Ostrich is a secondary result of the loss of flight and is not comparable to or homologous with the morphology of this apparatus in the shoulder-girdle of so many reptiles, more especially those Cœlurosaurian and Pseudosuchian types which exhibit so many bird-like similitudes in the rest of their skeletal structure, and which there seem such justifiable grounds, as Broom himself, Osborn (1917), Heilmann (1926), and others have pointed out, for regarding as either co-lateral or direct ancestors of the avian class.

So also we must conclude, if we agree with Broom, that the short, flattened, quadrilateral coracoid with its coracoidal foramen is a degraded phase of the elongated and more cylindrical coracoid

Text-figure 18.



Coraco-scapular bar in ostrich embryo: A. Ten days old; B. Eleven days old. After Broom.

of the flying "proto-carinate ancestor," a conclusion which seems well-nigh impossible of acceptance, especially if we bear in mind that in the flightless *Mesites* of Madagascar, alluded to above, there is not only no sign of diminution in the length of coracoid but an actual exaggeration of it and of its cylindrical form, while yet the pelvis has had time to undergo the most marked alterations correlated with a cursorial habit.

Thus, against the view held by Broom that the ancestors of the Palæognathæ were birds capable of flight with elongated coracoids seem to be the following considerations.—

1. That in the ten-days' Ostrich embryo these latter bones are, as shown by Broom himself, short, broad, more or less quadrilateral and flattened structures, while the apparent formation of the coracoidal foramen by the gradual descent of the descending process of the scapula, as shown in Broom's figures, gives anything but a picture of what we might expect to find in a carinate form.

On the contrary, it seems to me that the sum total of the morphological details is wholly reptilian and comparable to what occurs in such forms as *Euparkeria capensis*, *Ornithosuchus*, or *Mesosuchus* as figured by Broom (1913, pls. lxxvi-lxxviii) and others.

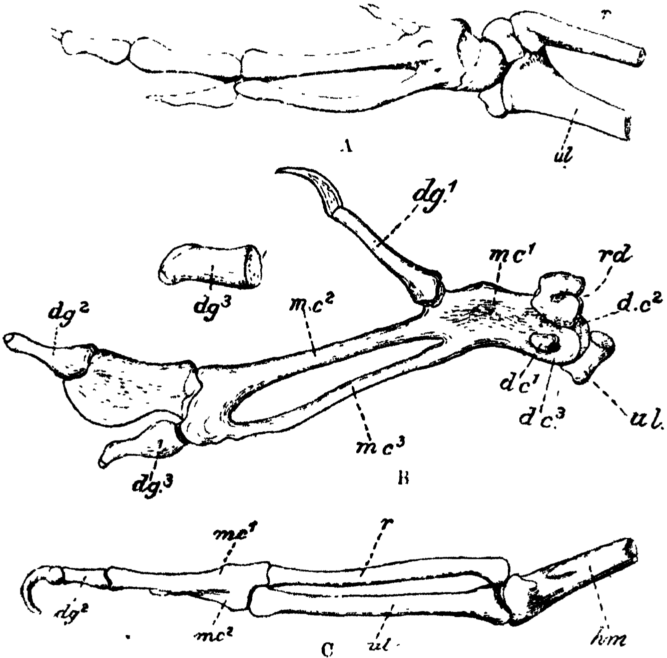
It seems evident, too, to judge by the recent work of Petronievics and a personal examination of the coracoid of *Archæopteryx* as now exposed in the original matrix, that this type of coracoid represents a pre-volant stage in avian evolution; or perhaps one of many pre-volant stages. To use such a word as "pre-volant" in connection with *Archæopteryx*, generally regarded as the earliest flying bird known, may appear to be unjustified, but it seems to me that the very long and attenuated bones of the manus of this remarkable bird could not possibly have supported the strain of ten or twelve well-developed primaries while beating the air without instant disaster.

Heilmann (1926) has suggested that the sternum of both *Archæopteryx* and *Archæornis*, as in all reptiles, was unossified, which may account for the fact that no trace of this structure has been discovered in either fossil. If this was so, it is additional ground for the strong presumption that neither of these birds was capable of anything more in the way of flight than a simple gliding, or a jump and then a glide, any beating of the wing being precluded without a strong ossified *point d'appui* for the major pectoral muscles which probably existed in a very rudimentary condition.

If, however, we make the supposition that the reptilian bird with gliding movements like *Archæopteryx* and the truly volant carinate bird represent co-lateral branches descended from a common flightless ancestor, then we might justifiably hold the view that the lengthening of the coracoid, together with the ossification of the sternum, the acquisition of the keel, and the shortening, strengthening, and keying-up of the bones of the manus were all factors independently developed by the carinate volant branch subsequent to their divarication from the primitive avian stock.

In the case of the Struthiones neither a lengthening of the coracoid, the acquisition of a keel, nor of the essentially avian centres of ossification proper to the sternum have been developed: they are conspicuous by their absence; while as regards the keying-up, strengthening and shortening of the bones of the manus, a phenomenon obviously secondary to the acquisition of flight, there is but little evidence (see text-fig. 19), for if a comparative examination of the various existing flightless struthionic forms is made it will be found that specialisation in this direction has proceeded farthest in *Rhea* and next in *Struthio*, while it is obvious that in these two forms, as well as in *Dromæus*, in which the specialisation is hardly noticeable, the degree of morphological change exactly corresponds to the extent

Text-figure 19.



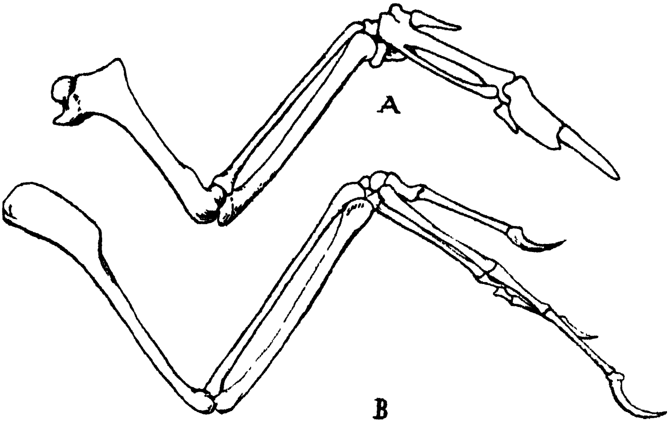
Bones of manus of (A) *Struthio*, (B) *Rhea*, (C) *Dromæus*, to show more generalised condition approaching that of *Archæopteryx* (text-fig. 20 B), or embryo Hoatzin (text-fig. 21 A), as compared with the specialised volant condition of adult Pigeon (text-fig. 20 A) and adult Hoatzin (text-fig. 21 B). After Kitchin Parker.

to which the wings are used as a lifting or balancing organ in each case.

2. If, in common with the generality of writers upon the subject, we are to postulate a flying ancestor for the Palæognathæ, it seems evident that we must also presume that in that ancestor there could have been no fusion between the coracoid and scapula, so that if the fusion noted by Broom between these two bones in the ten-days' embryo Ostrich is not evidence of a primary

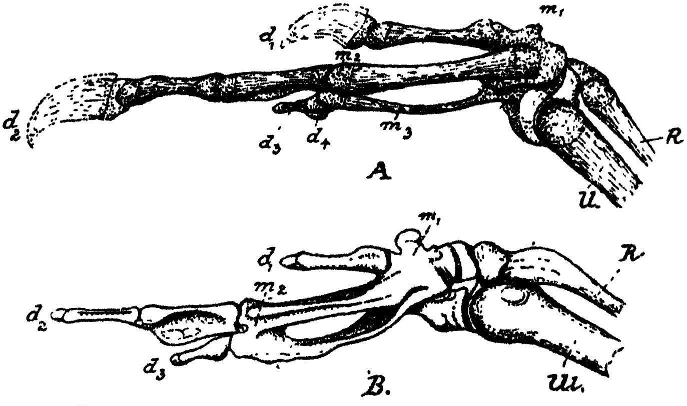
reptilian condition, it must indicate a subsequent return to a pseudo-reptilian condition as the result of the loss of flight. This latter alternative seems inconceivable since it is not only not seen in those avian types in which the power of flight has been obviously lost, but we also have to account for the presence of the foramen coracoideum and the pre-coracoidal element in the complex.

Text-figure 20.



Bones of manus in (A) Adult Pigeon, (B) *Archæopteryx*. After Heilmann.

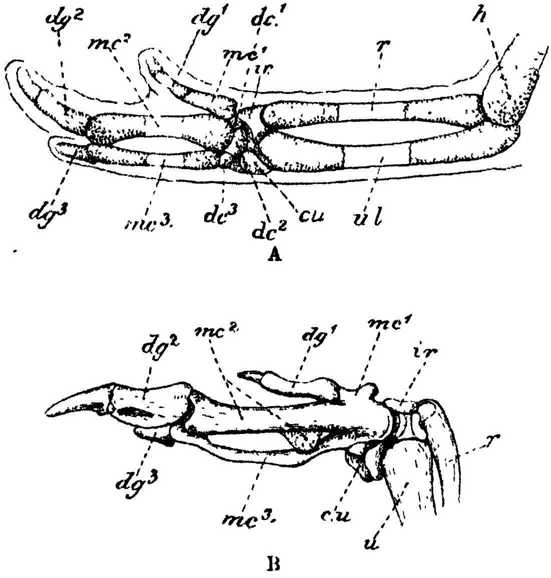
Text-figure 21.



Bones of manus in (A) Embryo Hoatzin, (B) Adult Hoatzin.
After Kitchin Parker.

3. Broom (1906, *loc. cit.* p. 356) insists, however, that though many have regarded this latter process as a precoracoid, "we may be pretty sure, from what we now know of the morphology of the precoracoid in primitive reptiles, that the bone in the Ostrich is an anterior process of the scapula, and is in no way homologous with the true precoracoid of early forms." Whether, however, we regard it as pre-scapular or pre-coracoid it seems hard to believe that this conspicuous and characteristic feature of the shoulder-girdle in "one of the most primitive birds at present alive" is not reptilian-derived but has been, so to speak, "re-incarnated" in the bird, not as a homologue of the reptilian coracoidal bony offshoot, but as its analogue. Such occurrences, as we all know, may occur, but my point is that if it is so in this instance it seems strange that the "pre-coracoid" is seen in its most marked form of development in the most ancient group of existing birds, and, moreover, that the same process of bone takes part in the "reproduction" of the coracoidal foramen in a way which so exactly recalls the method of formation of this foramen in such primitive reptiles as *Euparkeria* and *Ornithosuchus*.

Text-figure 22.



A. Manus of embryo fowl.
B. Manus of adult fowl. After Kitchin Parker.
Compare with text-figures 19 to 21.

Moreover, by the time the carinate Neognathæ had reached the zenith of their flying capabilities the coracoid had become so specialised that the pre-coracoid dwindled to a rudimentary fraction of its former size.

4. Broom, like Miss Lindsay, found no trace of a clavicle in the ten-days' embryo Ostrich; but in the "flying ancestor," he says, "there would doubtless be a large clavicle.' If this had been so it seems not unreasonable to think that we should have found indications of one in the embryo. That clavicles are not found in the embryo Ostrich seems pretty good evidence that they were not present in the struthious ancestor.

There is, however, a difficulty in the case of the Emu, which has rudiments or vestiges of clavicles on either side, otherwise there might have been justification for applying the above assumption to the whole of the known struthious forms, since no other member of the Struthiones, living or fossil, had, so far as is known, any trace of clavicles.

It is necessary, however, to ask oneself the question at this juncture, whether the vestiges of clavicles seen in the Emu are not in reality and in truth vestiges of reptilian clavicles and not of an avian furculum, and to reflect that the clavicles are preformed in membrane and are very prone to disappear. They have disappeared in the Cœlurosauran dinosaurs, for example, which are presumably a specialised offshoot from the Pseudosuchians or some allied group, while in the Pseudosuchians they are present.

If, therefore, we formulate the proposition that the Palæognathous ancestor was derived from some generalised reptilian group ancestral to both the Pseudosuchians and Cœlurosaurans, there seems no more improbability in the supposition that the clavicles dropped out when the struthious ancestor originated than in the actual fact that they did drop out in the case of the Cœlurosaurs and remained in the Pseudosuchian, while the cropping up of vestigial remnants of clavicles in the Emu is only comparable to other hereditary phenomena.

THE PALATAL REGION.

In the adult stage the palate of every known struthious form, either living or extinct, except the one genus *Struthio*, differs from the adult Neognathous palate in the fact that the pterygoid process of either side makes junction with the posterior cornua of the vomer. In doing so they "ride off" the palatine bony plate and prevent it forming contact with the basisphenoidal rostrum or with its fellow of the opposite side, a contact which is effected in the Neognathæ.

In addition, the palatine makes a junction with the pterygoid not by a "cup and ball" joint as in the Neognathæ, but by a plain overlapping squamosal suture. Kitchin Parker, many years ago, called attention to this peculiarity as also to the distal extension of the pterygoid—the hemi-pterygoid—which in the embryonic Neognathous bird extends forwards in a spike-like form much as it does in *Rhea*. As Pycraft has very clearly illustrated, not only does it extend forwards but it effects a junction, though feeble, with the vomer. Later on, after the hatching of the young bird, the identity of this distal end of the pterygoid in the Neognathous embryo is lost by reason of the fact that it becomes fused with, or merged into, the structure of the under surface of the palatine plate which, in its turn, has succeeded in moving inwards so as to effect a junction in the middle line with its fellow of the opposite side. A similar movement inwards may be traced in the Struthiones by a comparative examination of the morphology of the palatine plate in the adult Emu, admittedly the most primitive or generalised form in that group, and the like structure in the more specialised Rhea. To return, however, to the point at issue—at the same time as the hemipterygoid is becoming absorbed by the palatine plate a segmentation, solution of continuity, or "fracture" occurs at a point in the pterygoid corresponding to the hinder margin or free border of the palatine. At this point a glenoid joint is evidently formed between the pterygoid and palatine, so that with the absorption of the hemipterygoid and the appearance of this joint all trace of the former bone's connection with the vomer is lost.

Such, in brief, is the history which is concerned with the evolution of this portion of the Neognathous palate. I have introduced it here not for its own intrinsic interest, enhanced as it has been by Pycraft's careful study of its story, but because in the Struthiones, more especially in the Rhea, it is possible to trace some of the steps which led to the evolution of the Neognathine palate from the more primitive Palæognathine. For instance (1) the inward movement of the palatines towards their Neognathine objective in the middle line, (2) the cutting off of all contact of the vomer with the pterygoid, a contact which, as we have already seen, is essentially characteristic of the Struthiones; while, as Pycraft has already pointed out, there are other steps of secondary interest such as the shortening and forward movement of the vomer and the relative shortening of the basi-sphenoidal rostrum.

In one word, we have in the palatine morphology of the struthious *adult* the same phase of evolution as is obvious in the *embryos* of the Neognathæ. One struthious palate may show advances from an evolutionary point of view on the other, but it is strictly true to say that the evolution of the adult struthious palate has, in comparison with the palates of all Neognathous birds, been arrested in an "embryonic" stage. As Kitchin Parker long ago pointed out, it is possible to derive from it all the other types of avian palate.

The only possible conclusion to be drawn, therefore, is that the struthious palate is more primitive than the Neognathous and that in it we have an accurate presentment of what the early avian palate was like.

Broom has given a figure of the palatal view of the base of the skull of *Ornithosuchus woodwardi*, one of the primitive reptiles belonging to the Pseudosuchia, and Heilmann has compared this with a figure of the palate of *Apteryx australis*. When we examine these two figures we can hardly fail to be struck with the homologies of the several parts, especially when we also note the prominent basipterygoid processes in *Ornithosuchus*, a prominence which is such a peculiar and striking feature in all the Struthiones. How then, we may ask, can it possibly be maintained, in the face of these facts appertaining to such a fundamentally important complex of basi-cranial structures, that the Struthiones are derived from a carinate ancestor? I use the word "carinate" as being here synonymous with "Neognathous," but it may be added that Pycraft, in his 'History of Birds' (p. 42), has stated, "as a matter of fact the raft-like character of the breast-bone [in the Struthiones] is of no real importance, no guide as to questions of affinity: it is a secondary, degenerate character, which has been independently acquired by many birds."

In my remarks on "The Sternum," I have shown that Miss Lindsay has proved by her study of the embryo Ostrich that the keel is not lost. It never existed. The raft-like character of the breast-bone in the Struthiones cannot therefore possibly be a secondary one independently acquired in this group, while it seems at least open to doubt if it was so acquired in such a group as the Stereornithes, which, unfortunately, we have not space to consider in this paper.

Basipterygoid Processes.

One of the most striking features of the base of the skull in all the known Struthiones without exception is the presence of very large and conspicuous basipterygoid processes. The presence of these processes has been described, with what we may take to be an absolute approach to the truth, as indicative of a primitive or reptilian condition. In the Neognathæ there are groups, such as the Charadriiformes, in some subdivisions of which they are present both in young and old (Limicolæ), while in others, such as the Laro limicolæ, they are present in the embryo and chick while absent in the adult, the loss being obviously secondary and due to specialisation. In the birds of prey again, *Serpentarius*, probably the most primitive, has them; so have the American Vultures, while in the Falconidæ they are absent. Beddard has called attention to the fact that a certain degree of co-relativity can be traced in the presence of basipterygoids and a primitive arrangement of the gut.

In the Struthiones the morphological details of the basipterygoids are so peculiar that the term "Struthious" may rightly applied to them.

The Quadrate Bone

In a paper published in the 'Ibis' (1926), in which the quadrate is specially dealt with, I have made some observations on this important structure whose relations to other basal structures of the skull in the Ostrich-like group of birds are so characteristic as almost to be synonymous with the term Struthious.

I do not propose, therefore, to offer any further remarks upon it here, except that in both the flightless Struthiones and the flying Tinamous the morphology of this structure is so essentially identical that it seems to preclude any question of its being in any way a secondary effect consequent on the loss of flight.

Whether its essentially reptilian characters are peculiar to the Struthiones and Tinamous or are only shared by these groups with the larger division of the Palæognathæ is a point which, although it seems likely, can only be settled by the acquisition of further fossil material.

At any rate this much seems true, viz., that the struthious quadrate holds very much the same relation to the Neognathous quadrate as the struthious palate does to the Neognathous or Euornithic, while it seems almost a platitude to remark that neither the struthious quadrate nor palate could possibly have been derived from the newer or more specialised Euornithic quadrate or palate. In this connection it is interesting to note that *Diatryma* (Lower Eocene), which Matthew and Granger (1917) regard as probably a derivative of normal Cretaceous Euornithes, has a form of quadrate which they consider as being somewhat intermediate between the Palæognathous and Neognathous. This conclusion is based on the fact that although the quadrate is single-headed it is bi-facetted. This, however, is a condition which, as I have already pointed out (*loc. cit.* p. 157), is far from being uncommon in the struthious assemblage.

The Sternum.

In the embryonic sternum of the existing Struthiones we find, with one exception, that only one pair of ossifying centres exist. These ossifying foci are symmetrical and they are situated, one on either side, in relation with the fused cartilaginous distal ends of the ribs. These fused distal ends of the thoracic ribs form a longitudinal membranous expansion on either side of the middle line, and as development proceeds gradually approach one another in the middle line, where they eventually fuse, thus forming the sternum or breast-plate.

To each of these ossifying centres the name of *Pleurosteon* has been given, and, with the exception of the Rhea, which has in addition a *pro-osteon* for the ossification of each of the anterior lateral processes, they represent the only pair of ossifying centres which exist in the sternum of the group under consideration.

In reptiles the breast-plate is either entirely absent or is exactly equivalent in form and structure to the sternum of *Æpyornis*.

Space forbids the inclusion of further remarks upon the sternum, but, in view of the above facts, I would ask is it possible to reconcile what is known as to the development and morphology of the struthious sternum with any theory which would ascribe the primitive peculiarities of the morphology to a retrogradation or degeneration secondary to the loss of flight?

THE STERNAL CALLOSITY.

I have already discussed the callosities of the struthious association in a former paper (1926), and I have there ventured the suggestion (p. 674) that "the sternal and pubic callosities may be relics inherited from the reptilian ancestors of birds (the Pseudosuchians, for example), which may have rested, when in the crouching position, with their breasts supported by some similar special modification of the epithelial scales of the fore-end of the sternum or of those over the pubis."

Struthio, *Dromæus*, *Casuarius*, and *Rhea* among existing Struthiones are all furnished with conspicuous sternal callosities, and from what we know of the fossil impressions indicating the method of crouching in certain primitive reptiles the inference seems justified that the sternal callosities in struthious birds not only indicate a very primitive condition, but would appear to suggest that they were primarily inherited and not likely to have been acquired after the usually postulated loss of flight following descent from Proto-Carinate ancestors.

THE VERTEBRAL COLUMN.

From the point of view of evidence for or against the opinion that the Palæognathæ are the degenerate survivors of some proto-carinate volant ancestor, the fact that they have a greater number of vertebræ than any other existing birds known seems to be a point which cannot easily be dismissed.

Mivart (1874, p. 385), in his memoir on 'The Axial Skeleton of the Ostrich,' gives the number of vertebræ as 56, made up as follows * :—cervical 17, cervico-dorsal 3, dorsal 5, dorso-lumbar 2, lumbar 8, sacral 3, sacro-caudal 8, caudal 10.

In *Dromæus* the total amounts to 55, in *Casuarius* to 59, in *Rhea* to 51. *Archæopteryx* had only some 50 vertebræ and 21 of these were caudal. Some of the higher placed arboreal birds have the smallest number of all birds.

Heilmann has recently demonstrated that as regards almost every osteological feature possessed by *Archæopteryx* and *Archæornis* they were, if possible, more reptilian than had been previously suspected.

---

* The fact that the nomenclature and classification given by Mivart are not in accord in all respects with the views of other zoologists does not affect the question.

That these two birds possessed the power of flight in the sense in which it is associated in our minds with modern birds seems, as I have attempted to show on p. 228, highly improbable.

If, therefore, we are, generally speaking, justified in regarding those birds with the largest number of vertebræ as older types than those possessing fewer, it is evident on this view that *Archæopteryx*, as Beddard (1898, p. 115) has already said, must be regarded as representative of a parallel branch to the existing birds and not as their ancestor. Similarly, it might be argued that in this respect the Palæognathæ were more nearly reptilian than any other group of birds.

It may be stated, however, that the Swan (*C. buccinator*) has four more cervicals than the Ostrich, while the sum total of its vertebræ comes to 53, so that as regards the total number in the various groups of Palæognathæ there seems to be no such number as to render their derivation from a volant ancestor a matter of impossibility.

The Dorsal Vertebræ.—In the genera *Struthio*, *Rhea*, *Casuarius*, *Dromæus*, *Apteryx*, *Dinornis*, *Emeus*, *Anomalopteryx*, and *Pachyornis* the dorsal vertebræ have a more completely free and independent existence as regards their spinous and other accessory processes than can be noted in any other birds I am acquainted with, with the possible exception of *Aptornis* and *Diaphorapteryx*. On the other hand, in the Tinamous the said vertebræ, with the exception of the last, have no such free and independent existence, there being a very conspicuous synostosis affecting the spinous processes. It may also be noted that this free condition of the dorsals in all the genera quoted above, with the possible exception of the Ostrich and Kiwi, is correlated with an entire absence of a pygostyle.

Pygostyle.—As is well known, in almost all the Neognathæ the last six or seven caudal vertebræ coalesce into a subtriangular upright plate of bone which goes by the name of the pygostyle or ploughshare bone, and which gives attachment to the tail-feathers.

In *Rhea*, *Casuarius*, *Dromæus*, *Emeus*, *Dinornis*, *Pachyornis*, and *Anomalopteryx* there is no trace of a pygostyle as far as I have been able to discover from the material available. In *Apteryx* it has been said to have been occasionally observed (Newton, 1893–1896), but all that Jeffery Parker (1892, p. 78) says about it in the chick at the time of hatching is "but the 46th or last vertebra of the entire series is a broad trough-like bone, somewhat resembling the pygostyle of many birds." There is not a trace of it in the mounted skeleton in the British Museum.

In the Ostrich the most distal caudal vertebra is so modified that there is an approach to what might be regarded as the commencement of a pygostyle. The caudal vertebræ anterad of this do not exhibit to my mind any modification in this direction. But the Ostrich uses its wing in an attempt at a sort of pseudo-flight and presumably uses its tail to steer with. Its tail-feathers are well developed.

The evidence, then, for a previous existence of a pygostyle in the Struthiones does not appear to be very strong, and one would have been inclined to the view that had these birds originally possessed a tail comparable to that of the flying Neognathæ it would at least have been retained by the more cursorial as an aid to balance and steering, not necessarily in its original perfection, but in some modified and practically useful shape. *Struthio's* "pygostyle" may be a secondary modification.

Newton, however, to quote him again, says:—"*Hesperornis*, the Ratitæ, and Tinamidæ retain, even when adult, thirteen free caudal vertebræ, which diminish in size towards the tip of the tail, and thus these birds present in that respect an embryonic condition, though it is more probable that in them the absence of a pygostyle has been brought about in a secondary way by the gradual loss or reduction of once strongly-developed rectrices, than that it should be the retention of a primitive feature."

Why the Tinamous, however, some of which fly well, should have parted with "strongly-developed rectrices"* and a pygostyle it is difficult to see.

THE INTESTINAL TRACT.

As is well known, there is a very considerable degree of variation in the form and complexity of the intestinal loops and tracts as met with in birds, and Beddard and Gadow by their prolonged researches demonstrated the taxonomic value of this aspect of avian morphology.

Chalmers Mitchell (1896 and 1901) continued this work in two classical and exhaustive papers on the subject, and perhaps the most valuable feature of his investigations was that they were carried out subsequent to a preliminary enquiry as to what might be justly considered the ancestral or generalised type upon which all the various modifications characteristic of the many avian groups had been moulded. Very briefly stated he found that the condition of the gut in *Palamedea cornuta*—the Horned Screamer of South America—might be taken as closely representing the ancestral type. "I propose," he said, "to call such a condition 'Archicentric,' implying that it represents a primitive ancestral, or central condition, from which the condition to be found in other cases have diverged."

In the two papers cited he gives figures illustrating the arrangement of the intestinal tract in *Casuarius*, *Struthio*, *Rhea*, *Apteryx*, and the Crypturi.

As regards the first four genera, with which may be included *Dromæus* as only differing from *Casuarius* in minor modifications, he goes on to say:—"When correction has been made for the obviously homoplastic modifications in the intestinal tract of the Ratites—that is to say, when a reduction has been made in the case of the larger forms for size and in the case of the herbivorous forms,—it is plain that while all are archicentric, the Casuarii are by far the least modified, and that in this, as in many other characters, they deserve the position assigned them as extremely primitive types. *Struthio* and *Rhea* are more modified, and the modification is in the same direction in each. *Apteryx* stands somewhat apart from the others, the specialisation of the supraduodenal loop being well marked in it.

---

* Beddard (1898, p. 492) says: "There are, at most, faint traces of a ploughshare bone in the *Tinamou*."

"The general character in all, however, is so plainly archicentric that no argument can be drawn from the intestinal tract for or against the polyphyletic nature of the group."

As regards the Tinamous he finds that the type of the intestinal tract "is markedly apocentric," and that it is as possible that it might be derived from the Ratite gut as from that of any other archicentric form, but that, so far as the character of the intestinal tract goes, there is no special reason to associate the Tinamous with the Ratites, nor, for that matter, with the Galliformes.

THE VENTRICULAR MODERATOR BAND.

Beddard, in his 'Structure and Classification of Birds,' calls attention to the interesting fact that Rolleston, in his Hunterian lecture, described and figured a muscular pillar in the heart of the Cassowary which unites the free and fixed walls of the right ventricle, and to which he gave the name of the moderator band. It was Rolleston's suggestion that this moderator band, which is also found in Deer and other running animals, was a mechanism for increasing the power of the ventricle to contract, thus ensuring a more rapid and regular flow of blood into the lungs. It is, in fact, as is now well known, a characteristic feature of the heart of running animals.

This band may, of course, have been independently acquired as the result of the necessity for a free-running habit secondary, as some would say, to the loss of flight, but it appears to me just as likely, if not more so, that the moderator band might have been directly inherited from fast-running and reptilian ancestors.

THE SYRINX.

In reptiles there is no specialisation of the tracheal or bronchial rings at the bifurcation of the trachea corresponding to that which forms the voice-organ or syrinx of birds, to which class it is entirely peculiar. It says a good deal, therefore, for the reptilian simplicity, or want of differentiation, of this part of the respiratory tube in the struthious assemblage that it was formerly maintained by authors that a syrinx did not exist in this order. That such an assertion was incorrect was amply demonstrated by Forbes (1881, p. 778), but, nevertheless, the syrinx of the Ostrich (*Struthio*) is so simple and generalised that it differs from the most simple or typical of all avian voice-organs in the absence of tracheo-bronchial muscles as well as a pessulus, while the amount of specialisation of the last tracheal rings is reduced to the smallest possible amount.

"The genus *Apteryx*," says Forbes (*loc. cit.*), "in the simplicity of its lower larynx (syrinx) stands on the same level as *Struthio*." In *Casuarius* and *Dromæus* we have exhibited an advance beyond *Struthio* or *Apteryx* in the evolution of this specialised portion of the trachea, while in the Rhea there occurs a condition of things as to the syringeal nature of which there can be no mistake. It is plain, therefore, that in the living members of the Struthiones we have, as regards the organ of voice and its complexity, not only no evidence of degeneration, but obvious instances here and there of an ascent from a simple generalised organ to one which merits beyond any doubt the right to be characterised as a true syrinx.

PHYLOGENETIC OR SYSTEMATIC STATUS OF THE STRUTHIOUS ASSEMBLAGE AND THE RELATION THERETO OF THE TINAMOUS (CRYPTURI).

The length to which this paper has already, and of necessity, attained unfortunately precludes anything but the briefest summing up of this interesting and important problem.

As pointed out by Prof. Newton (1893–1896, Introduction, p. 100), the great novelty of Prof. Furbringer's treatment of the Ratitæ ('Untersuchungen zur Morphologie und Systematik der Vogel,' 1888) does not lie in a denial of their existence as a distinct subclass, but in his demonstration of their being the retrograde descendants of volant ancestors and in the view that they diverged at different epochs, so that the various component groups are not homogeneous but each had an independent pedigree. Have we, then, in the face of this authoritative pronouncement, any right to regard the struthious assemblage as a natural group, and, if so, what is the exact relationship borne to it by the Tinamous?

Stating the case as briefly as possible, we are faced with the fact that on fewer than seven divisions or families of that assemblage, commonly known as the Moas, Rocs (Æpyornithidæ), Kiwis, Emus, Cassowaries, Ostriches, and Rheas, nearly all of them occupying areas of distribution which are almost as isolated as it is possible to conceive, are characterised by the possession in common of a long series of morphologically similar features.

In the possession of these anatomical characters they not only differ from any other group of existing birds, but it seems impossible to resist the conclusion that the characters bear the undoubted impress of a primitive and reptile-like stamp.

Under such headings as "Feather Structure," "The Palate," "The Quadrate," "The Sternum," and "Coraco-scapular Bar," some of these characters have already been noticed and described in some detail, while some fresh observations have been made. We may here briefly refer to others, such as the reptilian conformation of the pelvis, the late closure of the cranial sutures, the frontal exposure of the ethmoid, the large size and relationship of the basipterygoid processes, the absence of a pygostyle and a tufted oil-gland, and the presence of sternal callosities *.

It would, however, be quite feasible, and possibly justifiable, to argue that the possession of such characters in common only prove one thing, viz., the primitive or palæognathine origin of all the groups in question; for it is obvious that the possession in common of a long series of primitive or reptilian features might not necessarily indicate descent from a common ancestor or that the Struthiones represent a natural order †.

When, however, as often happens, we are faced with a predicament of this kind and, while having at hand an accumulating mass of evidence all apparently pointing to one probable conclusion, are yet in doubt as to the final verdict, it is often an apparently insignificant fact, or a series of them, which finally brings down the scale to one side or the other.

I will mention two or three such facts:—

(1) In the Kiwis of New Zealand (*Apteryx*), the sciatic artery and nerve are superficial to and run parallel with the insertion of the accessory femoro-caudal muscle, along the linea aspera of the femur, *as in most birds*; but they perforate the muscle near the sciatic notch, leaving a small portion of it above them, *a perforation only to be noted in the rest of the Struthiones and in the Tinamous* (*cf.* Garrod, 1873, p. 643). Moreover, this perforation is correlated with the very peculiar and additional accessory femorocaudal muscle only met with in these two groups of birds.

(2) All the Struthiones have cæca which, unlike any other birds known, are inserted into the rectum by a common orifice.

(3) There is a certain physiological character—the habit of "kicking forwards" possessed, as everyone knows, by the Ostrich (*Struthio*) of Africa. Such a character, taken by itself, would naturally appear to have little genetic importance. When, however, we find that it is possessed by no other birds *except* the Rhea of South America, the Emu of Australia, or the Kiwis of New Zealand, it is bound to arrest our attention, for it seems inconceivable that this habit of attack or defence could have been independently acquired in four widely separated countries.

(4) There is a remarkable similarity in nesting habits, especially in the behaviour of the cock bird, in all the struthious families except that of the Kiwis, which are very specialised as regards their mode of life.

Nathusius found such practical identity in the structure of the eggshell between *Rhea* and *Dinornis* that he proposed to place them in the same genus.

(5) The habit of falling forwards and resting on the forepart of the sternum (sternal callosity)—crouching, in other words—is very characteristic of the Struthiones. Fossil imprints lead to the assumption that some bipedal dinosaurs did the same.

---

* In *Apteryx* there is an indication only of a callosity.

† No discussion of the pelvic and hindlimb has been attempted as this would have carried this paper to too great a length.

Taking, then, all these similarities, both morphological and physiological, it seems altogether inconceivable that they would have been possessed in common, and in such a remarkable degree, by the various struthious families had these last diverged, as Fürbringer maintained, at different epochs or even different geologic horizons. Not only are these similarities very remarkable, but it seems even more remarkable still that in families separated by such vast distances of space and time specialisation or modification is not more evident than it actually is. In a word, is it possible to believe that all the groups which we have mentioned above are so many isomorphs ?

The Tinamous, on the other hand, although presenting so many Palæognathous, if not struthious, characters may well be regarded as having diverged from the avian stem at a later epoch than the Struthiones ; for in all those structures, osteological or myological, concerned with the function of flight and including even the perfected volant armature of the feathers, they are "Neognathous," using that term as synonymous with "carinate." so that here, indeed, and in all probable truth, we get the manifested result of a more recent origin from the avian stem, viz., specialisation or evolution in the direction of flight.

SOME CONCLUSIONS

(1) That the distribution in time and space of the Struthiones, especially as concerns the typical ostriches (*Struthio* and its allies), enhances the importance of these birds as a subclass sharply differentiated from all other birds.

(2) That feathers merely represented by scale-protected downy protoptyles were acquired when the primitive bird was still non-volant. But for these feathers the proto-avian fore-limb must have been closely similar to the fore-limb of its putative co-lateral Pseudosuchian reptilian ally. It is, I believe, from such an early stock that the Struthiones were directly derived.

(3) That, contrary to the opinion expressed by Fürbringer, all the evidence points strongly to the conclusion that the Struthiones represent a perfectly natural group descended from some common ancestor which left the main avian stem before flight had been attained.

(4) That where degeneration, retrogression, or specialisation has taken place in the struthionic fore-limb it has been a degeneration, retrogression, or specialisation of the primitive, generalised non-volant sauropsidan fore-limb and not of a volant carinate wing.

(5) That the characters which constitute the general make-up of the Struthiones represent, practically invariably, primitive or almost "embryonic" characters indicative of an early phase in the evolution of the true bird ; and that to regard such characters as degenerate or retrogressive is not justified by the evidence. In a word, the Struthiones represent persistent primitive types only secondarily adapted for a special mode of life.

(6) That the adults of the existing Struthiones are clothed in prepennal down and have not reached a much more advanced stage of development than the downy chick of a fowl.

(7) *Archæopteryx* and "*Archæornis*" are regarded as having left the main avian stem at an earlier (more reptilian) stage of evolutionary progress than the Struthiones; that they then became specialised for an arboreal existence, but, although successful in developing volant wing- and tail-feathers, failed to attain to the accomplishment of anything but a gliding form of flight, and, in fact, proved to be one of Nature's blind-alley failures. From the point of view of the evolution of perfect flight they may, in practical fact, be ranked as having gone one or more better than the Pterosaurs and one or more less than the true volant birds.

In conclusion, I would like to take this opportunity to express my very great indebtedness to Miss Dorothea Bate, in charge of fossil birds in the Department of Geology, British Museum, for the ready and valuable assistance she has continually given me in the preparation of this paper. To Colonel Morley Knight I am indebted for the fine series of Rhea embryos which he specially procured at my request, and to Lord Rothschild for his constant interest and the loan of a splendid series of fossil rails.

LIST OF WORKS REFERRED TO.

AMEGHINO, F. 1891. "Enumeracion de las Aves fosiles de la Republica Argentina." Rev. Argent. Hist. Nat. i. pp. 441–435.

ANDERSSON, J. G. 1923. "Essays on the Cenozoic of N. China." Mem. Geol. Surv. China, ser. A, no. 3.

ANDREWS, C. W. 1896. "On a Skull, Sternum, and Shoulder-Girdle of *Æpyornis*." Ibis, pp. 376–389, pls. viii., ix.

—— 1904. "On the Pelvis and Hind-limb of *Mullerornis betsilei* M.-Edw. & Grand.; with a Note on the Occurrence of a Ratite Bird in the Upper Eocene Beds of the Fayûm." Proc. Zool. Soc. London, pp. 163–171, pl. v.

—— 1910. "Note on some Fragments of the Fossil Egg-shell of a large Struthious Bird from Southern Algeria," pp. 169–174 in Rothschild, 1910.

ANDREWS, ROY CHAPMAN. 1926. "On the Trail of Ancient Man."

BEDDARD, F. E. 1898. The Structure and Classification of Birds. London.

BRANDT, A. 1873. "Ueber ein grosses fossiles Vogelei aus der Umgegend von Cherson." Bull. Acad. Imp. St. Pétersb. xviii. pp. 158–161.

BROOM, R. 1906. "On the Early Development of the Appendicular Skeleton of the Ostrich." Trans. S. Afr. Phil. Soc. xvi. pp. 355–366.

—— 1913. "On the South African Pseudosuchian *Euparkeria* and Allied Genera." Proc. Zool. Soc. London, pp. 619–632, pls. lxxv.–lxxix.

CHANDLER, A. C. 1916. "A Study of the Structure of Feathers with Reference to their Taxonomic Significance." Univ. Calif. Pub. Zool. vol. xiii. pp. 243–396, pls. xiii.–xxxvii.

DE VIS, C. W. 1884. "The Moa (*Dinornis*) in Australia." Proc. Roy. Soc. Qd. i. pp. 23–28, pls. iii. & iv.

—— 1888. "A Glimpse of the Post-Tertiary Avifauna of Queensland." Proc. Linn. Soc. N.S.W. iii. pt. 2, pp. 1277–1292, pls. xxxiii.–xxxvi.

—— 1891. "Residue of the Extinct Birds of Queensland as yet detected." Proc. Linn. Soc. N.S.W. vi. pp. 437–456, pls. xxiii.–xxiv.

Duerden, J. E. 1920. "Methods of Degeneration in the Ostrich." Journ. Genetics, Cambridge, ix. pp. 131-193, pls. v., vi., 8 text-figs.

Ewart, J. Cossar. 1921. "The Nestling Feathers of the Mallard, with Observations on the Composition, Origin, and History of Feathers." Proc. Zool. Soc. London, pp. 609-642, pls. i.-x.

Forbes, H. O. 1891. "On Avian Remains found under a Lava-flow near Timaru, in Canterbury." Trans. N.Z. Inst. xxiii. pp. 366-372, pl. xxxvi.

—— 1893. "A List of the Birds inhabiting the Chatham Islands." Ibis, pp. 521-546, pls. xiv., xv.

Forbes, W. A. 1881. "On the Conformation of the Thoracic End of the Trachea in the 'Ratite' Birds." Proc. Zool. Soc. London, pp. 778-788.

Fürbinger, M. 1888. Untersuchungen zur Morphology und Systematik de Vogel.

Gadow, H. 1888. "Remarks on the Numbers and on the Phylogenetic Development of the Remiges of Birds." Proc. Zool. Soc. London, pp. 655-667.

Garrod, A. H. 1873. "On certain Muscles of the Thigh of Birds and on their Value in Classification." Proc. Zool. Soc. pp. 626-644.

Gunther, A. 1868. "Contribution to the Anatomy of Hatteria (Rhynocephalus Owen)." Phil. Trans. Roy. Soc. clvii. pp. 595-629, pls. xxvi.-xxviii.

Hébert, E. 1855. "Note sur le Tibia du *Gastornis parisiensis*," pp. 579-582 "Note sur le Femur du *Gastornis parisiensis*," pp. 1214-1217. C. R. Acad. Sci. xl.

Heilmann, G. 1926. The Origin of Birds. London.

Lindsay, B. 1885. "On the Avian Sternum." Proc. Zool. Soc. London, pp. 343-357, pls. xxix.-xxxii.

Lowe, P. R. 1924. "On the Anatomy and Systematic Position of the Madagascan Bird *Mesites* (Mesœnas)." Proc. Zool. Soc. London, pp. 1131-1152.

—— 1926. "On the Callosities of the Ostrich (and other Palæognathæ)." Proc. Zool. Soc. London, pp. 667-679, pl. i.

—— 1926. "More Notes on the Quadrate as a Factor in Avian Classification." Ibis, pp. 152 188, pl. ii.

—— 1928. "A Description of *Atlantisia rogersi*, the Diminutive and Flightless Rail of Inaccessible Island, with some Notes on Flightless Rails." Ibis, pp. 99-131.

Lydekker, R. 1891. Cat. Foss. Birds Brit. Mus.

Major, C. I. Forsyth. 1888. "Sur un Gisement d'Ossements Fossiles dans l'Île de Samos, comtemporains de l'Age de Pikermi." C.R. Acad. Sci. cvii. pp. 1178-1181.

Matthew, W. D., & Granger, W. 1917. "The Skeleton of *Diatryma*, a Gigantic Bird from the Lower Eocene of Wyoming." Bull. Am. Mus. Nat. Hist. xxxvii. pp. 307-326, pls. xx.-xxxiii.

Mecquenem, R. de. 1908. "Contribution a l'Étude du Gisement des Vertebres de Maragha et de ces Environs." Ann. d'Hist. Nat. Paléont. Paris, i. pp. 27-79, pls. iv.-ix.

—— 1925. "Fossiles de Maragha." Ann. de Paléont. tome xiv.

Milne-Edwards, A. 1867-71. Ois. Foss. de la France. Texte I. & II. Atlas I. & II. Paris.

Mitchell, P. Chalmers. 1896. "On the Intestinal Tract of Birds." Proc. Zool. Soc. pp. 136-159.

—— 1901. "On the Intestinal Tract of Birds: with Remarks on the Valuation and Nomenclature of Zoological Characters." Trans. Linn. Soc. London, Zool., viii. pp. 173-275, pls. xxi.-xxiii.

Mivart, St. G. 1874. "The Axial Skeleton of the Ostrich." Trans. Zool. Soc. London, viii. pp. 385-451.

Moreno, F. P., & Mercerat, A. 1891. "Catálogo de los Pájaros Fósiles de la República Argentina." Ann. Mus. La Plata, i.

Newton, A. 1893-96. A Dictionary of Birds. London.

NITZCH, C. L. 1867. "Pterylography." Ray Society (Trans.).

NOPCSA, Dr. BARON FRANCIS. 1907. "Ideas on the Origin of Flight." Proc. Zool. Soc. London, pp. 223–236, text-figs. 74–82.

—— 1923. "On the Origin of Flight in Birds." Proc. Zool. Soc. London, pp. 463–477.

OSBORN, H. F. 1917. "Skeletal Adaptations of *Ornitholestes*, *Struthiomimus*. *Tyrannosaurus*." Bull. Am. Nat. Hist. xxxv. pp. 733–771, pls. xxiv.–xxvii.

OWEN. 1840. "On the Anatomy of the Southern *Apteryx*." Trans. Zool. Soc. ii. pp. 257–301, pls. xlvii.–lv.

—— 1866. Anatomy of Vertebrates. London.

—— 1869. Proc. Zool. Soc. London, p. 59.

—— 1872. Proc. Zool. Soc. London, p. 682.

PARKER, T. JEFFERY. 1882. "On the Skeleton of *Notornis mantelli*." Trans. N.Z. Inst. xiv pp 245–258, pls. xix.–xxi.

—— 1892. "Observations on the Anatomy and Development of the *Apteryx*." Phil. Trans. Roy. Soc. London, clxxxii. B, pp 25–134.

PARKER, W. KITCHIN. 1864. "On the Osteology of the Gallinaceous Birds and Tinamous." Trans Zool. Soc. London, v. (1866) pp. 149–241, pls. xxxiv.–xlii.

—— 1868. "A Monograph on the Structure and Development of the Shoulder-Girdle and Sternum" Ray Society.

PETRONIEVICS, B. 1921. "Ueber das Becken, den Schulter Girtel und einige andere Teile der Londoner *Archæopteryx*." Genf, pp. 1–31, pls. i., ii.

—— 1926. "La Colonne vertébrale et le Coracoide gauche de l'*Archæopteryx* de Londres." (Résumé.) Ghlas Srpska Kra'evska Akademija, Belgrade, cxxvi.

—— 1927. "Nouvelles Recherches sur l'Ostéologie des Archæornithes." Ann. de Paléontologie, xvi. pp. 39–55, pls. v.–vii.

PETRONIEVICS, B., & WOODWARD, A. SMITH. 1917. Proc. Zool. Soc. London, p. 5.

PYCRAFT, W. P. 1898. "On the Morphology of the Palæognathæ." Trans. Zool. Soc. xv. pp. 149–290, pls. xlii.–xlv.

—— 1910. Animal Life, vol. ii. A History of Birds. London.

ROTHSCHILD, Lord. 1910. "On the Former and Present Distribution of the so-called Ratitæ or Ostrich-like Birds." Bericht V. Internat. Ornith.-Kongrez, Berlin.

ROVERETO, C. 1914. "Los Estratos Araucanos y sus Fósiles." Ann. Mus. Nac. Hist. Nat. B. Aires, xxv.

SHUFELDT, R. W. 1890. The Myology of the Raven. London.

STIRLING, E. C., & ZIETZ, A. H. C. 1896. "*Genyornis newtoni*, a Fossil Struthious Bird from Lake Callabonna, South Australia." Trans. Roy. Soc. S. Australia, xx. pp. 191–211, pls. iii.–v.

TEILHARD DE CHARDIN, PÈRE. 1926. "Fossil Man in China and Mongolia." Nat. Hist. N.Y. xxvi. pp. 238–245.

WRAY, R. S. 1887. "On some Points in the Morphology of the Wings of Birds." Proc. Zool. Soc. London, pp. 343–357, pls. xxix.–xxxii.

YULE, Sir HENRY. 1921. Travels of Marco Polo.

EXPLANATION OF THE PLATE.

Under surface of wing of Rhea chick, seven to ten days old, to illustrate a primitive wing (prepennal stage) or the apparent limit of wing-development reached by the Struthiones.

Note: (*a*) The complete absence of a patagium and (*b*) of any sign of degeneration as regards feathering.

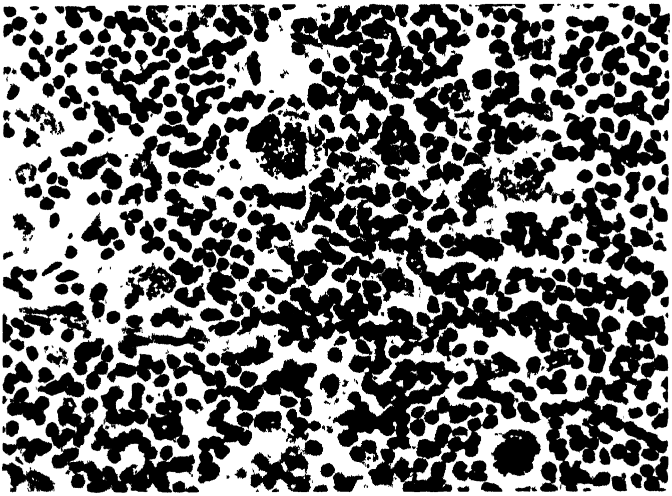
(*c*) The axillary bare space.

1

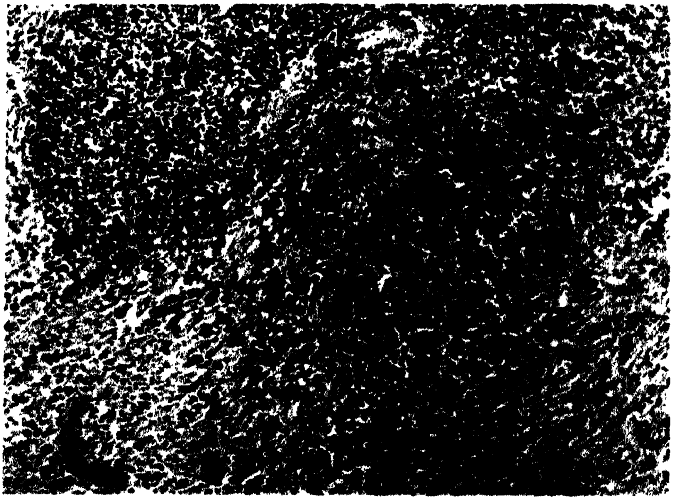
2

3

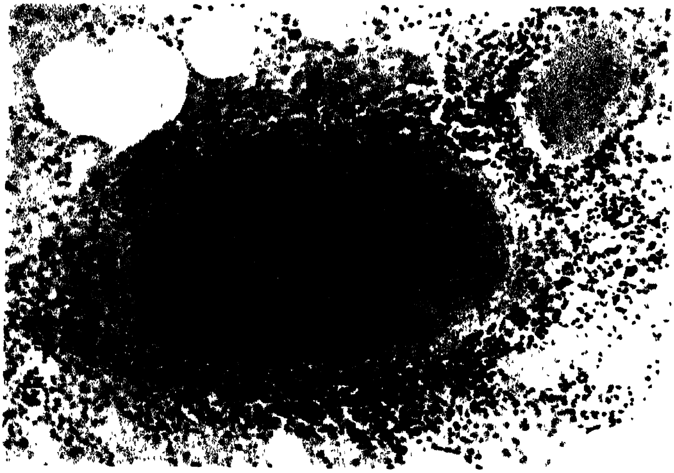
TUBERCULOSIS MARSUPIALS



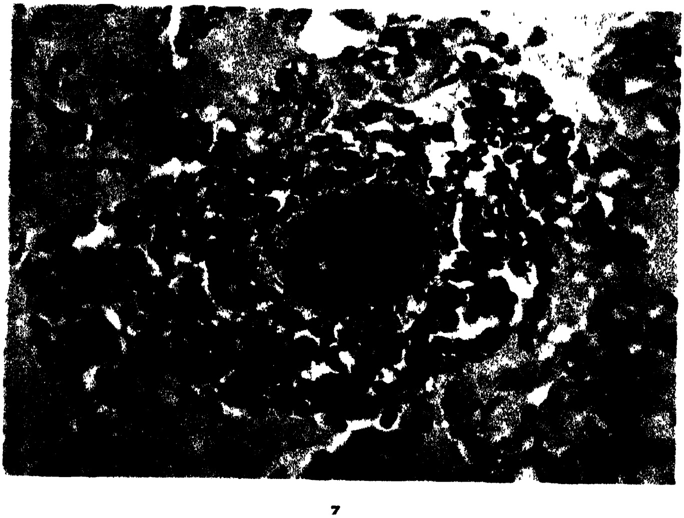
4



5



6



7

TUBERCULOSIS IN MARSUPIALS

12. Tuberculosis in Marsupials. By H. Harold Scott, M.D., F.R.C.P.Lond., F.Z.S., Milner Research Fellow in Comparative Pathology, London School of Hygiene and Tropical Medicine; Pathologist, Zoological Society of London.

[Received March 5, 1928: Read March 20, 1928.]

(Plates I.-III.*)

There are two main reasons for placing the following case on record in greater detail than is given in the routine account of autopsies carried out in the Prosectorium. The first is that Tuberculosis is by no means common in Marsupials, and is rarer still in the larger species, judging by the records of *post-mortem* examinations on animals dying in the Gardens; secondly, the type of infecting bacillus, as determined by Dr. Stanley Griffith, to whom some of the tissues were sent, was the Avian.

I have searched the records from the beginning of the present century, and can find fourteen referred to prior to that which forms the chief object of this paper, and one which received a brief note in the *post-mortem* records but is not referred to in the pathologist's report. Thus the total, if all are cases of genuine tuberculosis, amounts to sixteen since 1900 at least, and it will be seen that there is more than a little element of doubt in some of these.

The following is a complete list of all the marsupials diagnosed as exhibiting tuberculous lesions:—

1. 1905. Dormouse-Phalanger, *Dromicia nana*.
2. 1908. Opossum (? Azara's), *Didelphis azaræ*.
3. 1908. Rat-tailed Opossum, *Didelphys nudicaudata*.
4. 1908. Ring-tailed Phalanger, *Pseudochirus peregrinus*.
5. 1908. Vulpine Phalanger, *Trichosurus vulpecula*.
6. 1908. Rabbit-eared Bandicoot, *Peragale lagotis*.
7. 1909. Bennett's Wallaby, *Macropus bennetti*.
8. 1910. Bennett's Wallaby, *Macropus bennetti*.
9. 1911. Bennett's Wallaby, *Macropus bennetti*.
10. 1914. Tree-Kangaroo, *Dendrolagus ursinus*.
11. 1914. Viverrine Dasyure, *Dasyurus viverrinus*.
12. 1916. Lundie Opossum, *Didelphys albiventris*.
13. 1916. Rat-Kangaroo, *Bettongia penicillata*.
14. 1923. Rufous Rat-Kangaroo, *Æpyprymnus rufescens*.
15. 1924. Rufous Rat-Kangaroo, *Æpyprymnus rufescens*.
16. 1927. Kangaroo Island Kangaroo, *Macropus fuliginosus*.

---

* For explanation of the Plates, see p. 256.

It will be seen that nine of these are the small marsupials and only seven the larger—namely, three Bennett's Wallabies, a Rat-Kangaroo, two Rufous Rat-Kangaroos, and one Kangaroo Island Kangaroo.

The records of most are very scanty, but for purposes of future comparison and research it is thought advisable to give them here, such as they are, and so obviate the necessity for future investigators delving in past records to find what, in some of them at least, are very small needles in large bundles of hay.

1. The first is the Dormouse-Phalanger. This animal died on January 6th, 1905, having been in the Gardens 5 years 8 months. Beyond the single remark "Tubercle of liver" no details at all are given.

2. Opossum, dying on January 6th, 1908. Length of stay in the Gardens is not stated. The cause of death is given as Pulmonary tuberculosis. In both lungs were many scattered miliary tubercles, and the cervical glands were enlarged. No mention is made of any microscopical examination, either of smears or sections.

3. Ring-tailed Phalanger, dying on January 20th, 1908. This was a recent arrival, having been here only a fortnight. The lungs presented "several yellowish nodules, apparently on the outer surface of both lungs, raised above the surface. Lungs very congested otherwise. Other organs quite healthy." In this case microscopical examination was carried out and acid-fast bacilli seen.

4. Rabbit-eared Bandicoot, 2 months in the Gardens, which died on August 8th, 1908, of "Pneumonia of the left lung and enteritis." There was "early tubercle" of the spleen noted, the organ being enlarged and soft and "some very early miliary tubercles were present." No microscopical examination is recorded to confirm this. In view of these facts, that the spleen was the only organ involved, that only early miliary tubercles [unconfirmed] were present, it is possible, in the absence of microscopical examination, that the splenic enlargement was secondary to or associated with the enteritis and pneumonia, and that prominent Malpighian corpuscles were mistaken for "early tubercles"—a far from improbable error.

5. Rat-tailed Opossum, dying on September 2nd, 1908, after a residence of one year in the Gardens. In this instance the lungs, spleen, and kidneys were affected. Though again in this case there was no microscopical examination made (or at least mentioned), the characters of the lesions render the diagnosis almost certain. "*Lungs*: Right lung full of tubercular nodules, one of which was adherent to the chest-wall. . . . The left lung had also a certain number of tubercles of a smaller size. *Spleen* was enlarged, 1½ × 1 inches, and full of tubercular deposit. *Kidneys*: Both kidneys were full of tubercles and were acutely inflamed; in the right there was an abscess."

6. Vulpine Phalanger, 4 months in the Gardens, dying on October 23rd, 1908, with "tubercular abscess of lumbar glands." There was a large abscess infiltrating the right psoas muscle and extending from ribs to pelvis. The contents were thick, caseous, and inspissated pus. The spleen was enlarged and "full of caseous nodules," while the intestines were "bunched up and adherent to the abscess wall."

In this case also, there is little doubt, in spite of the fact that no microscopical examination was made, that the condition was tuberculous.

7. Bennett's Wallaby, 7 months in the Gardens, died on January 31st, 1909. The lesions noted in this instance were "in the right lobe of the liver a large caseating mass, 1½ in. in diameter, several smaller nodules scattered through the liver, and a group of much enlarged glands in the fissure. The mesenteric glands were enlarged and many were caseating." Very probably tuberculous and diagnosed as such, but without confirmation by microscopical examination.

8. The following is not mentioned at all in the Annual Report, but is recorded in the individual autopsies. A Bennett's Wallaby, nearly 2 years in the Gardens, was killed on May 2nd, 1910. The information on this is very meagre: all that is stated is "abscess under jaw, tubercle of spleen." "Spleen full of tubercular nodules, miliary." There was no microscopical examination made. This might possibly have been tuberculous, but a condition such as this has been found fairly frequently during the last three years, due not to tuberculosis but to Nocardial infection, going by the name of "Kangaroo Disease." A special paper recording several cases was read before the Society in 1925 *.

9. Another Bennett's Wallaby died on January 30th of the following year. Concerning this also there is more than a little doubt. The only facts noted are that it died of "broncho-pneumonia, nephritis, tubercle of spleen," and that the spleen was "congested and contained a number of tubercles of small size." No microscopical examination made. The doubt arises because no primary focus was found, miliary tuberculosis of the spleen alone is pathologically inconceivable in a mammal, and there was no confirmation as to any acid-fast bacilli being present.

10. On February 16th, 1914, a Viverrine Dasyure died of General tuberculosis after being in the Gardens for 9 months. The *post-mortem* findings are recorded in the following terms:—"Lungs very large and pale. Liver, spleen, kidneys, and intestines involved in a mass of tubercular growth; the spleen was enormous, 3½ × 1½ × 2 inches, and full of large nodules. Mesenteric glands very large. Intestines covered with nodules." No microscopical examination.

---

* H. Harold Scott, "A Streptothrix Disease of Wallabies," P.Z.S. 1925, pt. 3, pp. 799–814.

11. Tree-Kangaroo, 5 years 5 months in the Gardens, died November 29th, 1924. At the pyloric end of the stomach were several ulcers with undermined edges, and one of these was "adherent to a mass of caseating glands." The mesenteric glands were very large and caseating. Death was ascribed to "tubercular glands and ulcers of stomach," but again in this case there was no microscopical examination made.

12. Lundie Opossum, 7 months in the Gardens, dying June 16th, 1926, the cause of death being stated as "Tubercle of lungs and glands." There were numbers of milia in both lungs, but more in the left, while the bronchial glands were much enlarged and "full of tubercular deposits." Again no bacterial confirmation.

13. Rat-Kangaroo, 8 years in the Gardens, dying nine days after the last, on June 25th, 1916, with "tuberculosis of lungs and spleen." The "lungs contained many tubercles," and there was a single deposit on the edge of the spleen. No microscopical examination.

No more cases were found during the succeeding years, and the next instance recorded was by Dr. Lucas in 1923.

14. A Rufous Rat-Kangaroo, 14 months in the Gardens, revealing at autopsy "many small abscesses in the liver," and a swollen mesenteric gland "full of greenish pus which contained tubercle bacilli." It was with reference to this case that Dr. Lucas wrote in his annual report*: "There was also a case of tuberculosis in a Kangaroo-Rat. It is doubtful whether tuberculosis in a marsupial has been recorded previously."

15. In the following year another Rufous Rat-Kangaroo, which had been 22 months in the Gardens, died from tuberculosis, apparently of respiratory origin, the lesions being limited to the thorax. The left pleura was adherent, the left lung pale and solid, and when cut was noticed to be fibrous and white. The right lung was congested and full of soft caseous abscesses not much larger than a pin's head. These were found full of tubercle bacilli." The lungs were sent to Dr. Stanley Griffith, who will probably record the type of organism associated.

For ease of reference the records which have been detailed above are here presented in tabular form. It will be noticed that prior to 1923 in only one instance, the Ring-tailed Phalanger (No. 3), was any microscopical confirmation obtained, and this animal had been but a fortnight in the Gardens before it died, and therefore cannot have contracted the disease there.

---

* N. S. Lucas, "Report on the Deaths which occurred in the Society's Gardens during 1923," P. Z. S. 1924, pp. 293–296.

TABLE giving Details of Cases previously reported.

No.	Name.	Time in Gardens.	Organs involved.	Confirmation microscopically.	Reported by
1.	*Dromicia nana*	5 years 8 months.	Liver.	—	C. G. Seligmann.
2.	*Didelphys azaræ*		Lungs; cervical glands.	—	H. G. Plimmer.
3.	*Pseudochirus peregrinus*	2 weeks.	Lungs.	+	,, ,,
4.	*Peragale lagotis*	2 months.	Spleen.	—	,, ,,
5.	*Didelphys nudicaudata*	1 year.	Lungs, spleen, kidneys.	—	,, ,,
6.	*Trichosurus vulpecula*	4 months.	Lumbar glands, spleen.	—	,, ,,
7.	*Macropus bennetti*	7 months.	Liver, mesenteric glands.	—	,, ,,
8.	*Macropus bennetti*	1 year 11 months.	Spleen.	—	,, ,,
9.	*Macropus bennetti*	1 year 9 months.	Spleen.	—	,, ,,
10.	*Dasyurus viverrinus*	9 months.	Liver, spleen, kidneys, mesenteric glands.	—	,, ,,
11.	*Dendroldgus ursinus*	5 years 5 months.	Stomach, mesenteric glands.	—	,, ,,
12.	*Didelphys albiventris*	7 months.	Lungs, bronchial glands.	—	,, ,,
13.	*Bettongia penicillata*	8 years.	Lungs, spleen.	—	,, ,,
14.	*Æpyprymnus rufescens*	1 year 2 months.	Liver, one mesenteric gland	+	N. S. Lucas.
15.	*Æpyprymnus rufescens*	1 year 10 months.	Lungs.	+	,, ,,

The details of the case met with in 1927, the findings in which have instigated the present paper, are as follows:—

A female Kangaroo Island Kangaroo, *Macropus fuliginosus*, died on September 3rd, 1927, having arrived at the Gardens on June 19th, 1924. After a brief period of quarantine in the Sanatorium the animal was placed in the Kangaroo Sheds. Nothing was noticed to be wrong, there was little or no emaciation, and food was taken well up to the day on which it was found dead. At autopsy, which was carried out within an hour or two of death, old pleural adhesions were found on both sides, firmer and more extensive over the left lung, but not infiltrated with tubercles. In the lungs were sparse milia, but fairly equally distributed. There were some pleuro-pericardial adhesions, but the heart itself was normal. The thyroid was not affected. The intestine was macroscopically normal; there was no sign of any tuberculous infection of the alimentary tract, the mucosa being apparently quite normal and healthy. This is interesting in view of the lymphatic involvement. The liver, pancreas, and ovaries were unaffected, as were also the kidneys themselves, though in the angle just beneath the left adrenal there was a large caseated gland. The spleen was not obviously enlarged, but there were foci of deposit in its interior. The brain and meninges were intact.

The interest of the case is centred in the multiglandular involvement by tuberculosis. The axillary glands on the right side were enlarged and full of creamy, cheesy pus. One of these had become adherent to the shoulder-joint, and into this the abscess had opened so that the joint itself was distended with creamy pus, in parts caseated, and the surfaces of the articulating bones were a little eroded. There was a caseous abscess on each side of the top of the manubrium sterni involving the sterno-clavicular joints. At the root of the neck, by the left side of the trachea, was a glandular mass as large as a tennis-ball, converted almost into a sac of pus, and the cervical glands above it were swollen and purulent. There were no lesions in the mouth and the tonsils were healthy. The iliac and lumbar glands were enlarged and caseated, as were also those lying along the abdominal aorta, and at the cœliac axis they were aggregated to form an adherent caseous mass The spine was intact; no tuberculous disease of the vertebræ was discoverable, as may have been the case in No. 6, the Vulpine Phalanger, causing the psoas abscess. The thoracic duct was stuffed with caseous pus.

Smears were made from the pus in the shoulder-joint and that in the sterno-clavicular articulations, from the various gland-sites, the thoracic duct, the pulmonary lesions, and the spleen, and in all of them tubercle bacilli were present in enormous numbers. The thoracic portion of the body with its glands has been mounted as a permanent specimen, and fragments from the glands, spleen, and lungs were taken for microscopical examination;

portions of the organs were also sent to Dr. Stanley Griffith, who kindly wrote reporting that the bacillus isolated therefrom had proved to be of the *Avian type.*

The macroscopical appearances are shown in Pls. I. to III. Microscopically, the *glands*, when sections were stained by the Ziehl-Neelsen method, were seen to be packed with innumerable acid-fast bacilli; no giant-cells were seen. Larger cells (?endothelial) are seen stuffed with bacilli. The clumps of bacilli are evenly distributed throughout. *Spleen*: In the central parts there is caseation and necrosis; surrounding this the bacilli are massed in enormous numbers, which render the glandular splenic tissue unrecognizable. Towards the periphery they are still very numerous, but not so crowded as in the interior, and the spleen tissue can be distinguished. Again here no giant-cells are visible. *Lung*: The bacilli are focally distributed and, when present, are aggregated round the blood-vessels, not in the vessels themselves, nor are any seen in the alveoli, but occasionally in the walls of the latter, as would be expected in distribution, by way of the pulmonary arterioles; but the majority are perivascular, and are clearly seen in the lymph-spaces around the blood-vessels, where these are cut transversely.

There can be little doubt that the primary portal of entry was alimentary. It would appear that the infection was one repeated in small quantities at frequent intervals, if we may argue from the facts that involvement of the abdominal glands—mesenteric, lumbar, iliac, cœliac—was severe, whereas the mucosa of the intestine revealed no lesions. The thoracic duct was practically blocked with tuberculous deposit, and the pulmonary involvement was but slightly distributed, showing that the blockage of the thoracic duct was fairly complete; to the naked eye the characters of the lesions in the lungs were those of small milia. The general lymphatic distribution was evidenced not only by the extensive glandular involvement, but also by the presence of the accumulations (in the lungs) in the perivascular lymph-spaces. Briefly we may say that the infection was practically confined to the lymphatic system, the pyarthrosis of the right shoulder resulting from the opening into the joint of an abscess in an axillary gland which had formed adhesions to the capsule.

The question naturally arises as to the source whence the infection can have been contracted. Researches of recent times have tended to demonstrate the increasing importance of birds as conveyors of tuberculosis to mammals. In the Kangaroo Sheds, sparrows and other birds are quite commonly seen, and it is possible that the soil of the sheds has become infected by their droppings. Seeing that the animal had been in the Gardens for more than three years without presenting any symptoms, it is highly improbable that it was infected before arrival. Moreover, as stated above, the signs were indicative of frequent infection by bacilli in small numbers setting up a chronic disease rather than any massive dose causing acute tuberculosis.

EXPLANATION OF THE PLATES.

Plate I.

Fig. 1. Photograph of the lesions in the abdomen showing the enlargement of the lumbar glands, the swollen lymph-duct, and the mass at the cœliac axis.

Fig. 2. Photograph of the thoracic portion of the body showing the enlargement of glands in the thorax and at the root of the neck, with the large caseated mass to the left of the trachea and the cervical glands above it.

Fig. 3. Photograph of the bones of the right shoulder-joint showing the small erosions of the scapular surface.

Plate II.

Fig. 4. Section of gland crowded with acid-fast bacilli, the large cells being stuffed with them. There are no giant-cells seen. This crowding of mononuclear cells with bacilli resembles the stuffing of lepra cells with Hansen's bacilli in leprosy and is very frequent in avian tuberculosis.

Fig. 5. Section of spleen (low magnification) showing the caseated centre, the periphery crowded with acid-fast bacilli: the splenic tissue is recognizable only at the outer parts, where the bacilli are not so numerous as to mask the structure of the gland.

Plate III.

Fig. 6. Section of lung showing the perivascular distribution of the bacilli with small-celled infiltration. Giant-cells were present, though few, in this section, but they contained carbon particles and not acid-fast bacilli.

Fig. 7. Another field of the same section, under higher magnification, showing a vessel cut transversely and the perivascular distribution of the bacilli among the infiltrated small cells.

The first and third photographs were taken by Mr. F. H. Bond, all the others by Mr. F. Martin-Duncan, F.R.M.S., F.Z.S. I am greatly indebted to both these gentlemen for the care they have taken to reproduce the conditions present.

13. On the Giant Octopus of New Zealand.

By G. C. Robson, M.A., F.Z.S.

(Offered for publication by permission of the Trustees of the British Museum.)

[Received February 17, 1928 : Read March 20, 1928.]

(Text-figures 1–6.)

CONTENTS.

Page
1. Systematic (with description of *Macroctopus*, subgen. n.). 257
2. On the subdivision of the mantle-cavity in *Macroctopus*. 261
3. Bibliography 264

1. Systematic.

The giant Octopus represented by specimens from Dunedin and described as *Octopus maorum* by Hutton has received a fair measure of attention from systematists. A recent examination of two specimens of this interesting form in the British Museum has shown, however, that it is in many respects more remarkable than was at first suspected. For this reason I publish a complete description of its more important features, and assign to it a position as the type of a new subgenus. In the course of a revision of the Octopodidae, in which I am engaged, I have been convinced of the necessity of introducing a re-arrangement of the numerous species assigned to the genus *Octopus*, and for the time being it seems desirable to treat as subgenera the various distinct groups which can be distinguished within the latter.

Macroctopus, subg. n.

Octopods having the web largest between the dorsal arms and diminishing progressively in the subsequent interspaces. The septum is very extensive, and the orifice between right- and left-hand parts of the mantle-cavity is very small. The funnel-organ is absent, and the cephalic element of the locking apparatus is reduced to two small ridges on each side of the funnel. The head is very narrow. The gills are long and have 13–14 filaments aside. The sexes are dimorphic in that the suckers of the distal part of the arms in the female are reduced in size and converted into papillae.

Type of the subgenus: *Octopus maorum* Hutton (1880, p. 1) (in the Otago Museum).

OCTOPUS (MACROCTOPUS) MAORUM Hutton.

Octopus hectoris MS (? E. A. Smith), Brit. Mus. Colln. 1873.
Octopus maorum Hutton, 1880, p. 1.
Octopus maorum Hutton, 1882, p. 162.
Octopus maorum Parker, 1885, p. 586.
Octopus maorum Filhol, 1885, p. 520.
Octopus maorum Hutton, 1904, p. 57.
Polypus maorum Suter, 1913, p. 1064.

One specimen (♂) from Dunedin, New Zealand (Brit. Mus. 86.11.18,1) (*Dunedin Museum*).

One specimen (♂) from Wellington, New Zealand (Brit. Mus. 73.12.10.1) (*Colonial Museum*).

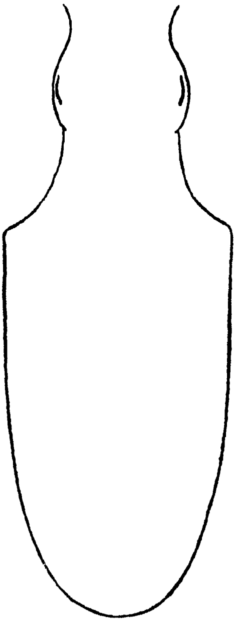
Distribution. Dunedin (*Hutton*); Stewart Island and Campbell Island (*Filhol*); Lyttleton, etc. (*Suter*); Wellington (*Brit. Mus.*).

The mantle (text-fig. 1) is narrow (the width is 39 per cent. of the length) and the head is very small, and, I think, the narrowest on record (26 per cent. of the mantle-length). There is a marked "neck" and a clearly-defined preocular constriction. The arms are usually in the order 1, 2, 3, 4, and are 81–87 per cent. of the total length. The mantle-aperture is very wide (Type C: *Robson*, 1926). The gills have a greater number of filaments than is usual (13–14 aside). The suckers attain a maximum diameter of 10–15 per cent. of the mantle-length. The web is unique in the genus in that it is largest in section 1–1 * and becomes progressively shallower from front to back. Section 1–1 is very much deeper than 4–4. The lateral arm-extensions are equally developed on the anterior and posterior edges of the arm. The *radula* (text-fig. 2):—The rhachidian has a symmetrical A_3 sequence (*Robson*, 1925). The adlateral has a very prominent cusp and a deep base. The second lateral has no entocone. Its heel is moderate; but the base is extremely deep. The third lateral is straight but has the extremity very much recurved. The marginals are degenerate and imperfectly seen. Hutton's description (1882) is not wholly in agreement with the above. In particular, he figures a small ectocone on the second lateral. I think this is an error and that he mistook the prominent external angle of the tooth for a cusp. The *septum* is very long (20 per cent. of the mantle-length); reference is made elsewhere to the subdivision of the pallial cavity. The *funnel* is only slightly prominent, and its free portion is only one-quarter of its total length. There is no funnel-organ and the organ of adhesion is very feebly developed. Instead of being formed of a complete transverse ridge crossing the base of the funnel from side to side, it consists of a pair of small ridges at the inferior external angles of the funnel. The *hectocotylus* (text-fig. 3) is long and spoon-like, and its ligula is furnished with obscure ridges. The *penis* (text-fig. 4) is very long and narrow. It has a moderately large and caruncculated

---

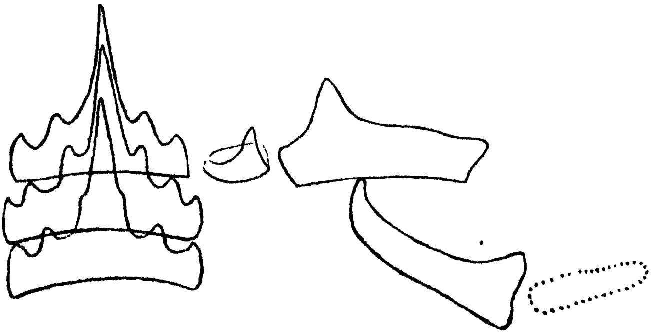
* The various interspaces between the arms are indicated by the serial number of the arms enclosing each section.

Text-figure 1.



Macroctopus maorum.

Text-figure 2.



Macroctopus maorum. Radula.

appendix. The peculiar reduction in size of the distal suckers of the female and their conversion into papillæ noted by Suter (*l. c.*) is, so far as I know, unique among Octopoda, though it is recorded in the male of *O. chierchiæ* (*cf.* also *Eledone*).

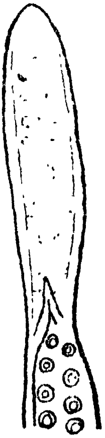
The external surface is smooth, but there are traces of an obsolete sculpture of low, broad warts. In spirit the colour is a pale ochre marbled with greyish purple.

The structure of the web and funnel, the long penis and septum, and the extraordinarily narrow head are a combination of characters quite unique in the genus. The head and mantle recall *O. macropus* somewhat, but the head is narrower and longer. The large specimen from Wellington does not differ in a very important degree from the Dunedin specimens. The mantle is not so elongate and is more saccular, but I am inclined to think that this is due to accidental distortion. The arms are notably longer, and the suckers are somewhat larger, the colour is more homogeneous and less marbled than in our Dunedin specimen. This specimen is larger than the average examples recorded (the largest example obtained previously measuring about 6 ft. 6 in. over all) (*Parker*, l. c. p. 586). The larger specimen was labelled *O. hectoris*, which I am compelled to assume is an MS. name. It cannot be traced in any literature. It is an interesting point that it was labelled as "*hectoris*," presumably by Mr. E. A. Smith, in 1873, and the MS. name of the species, which thus ante-dated Hutton's by seven years, may be due to him.

Dimensions (in mm.):—

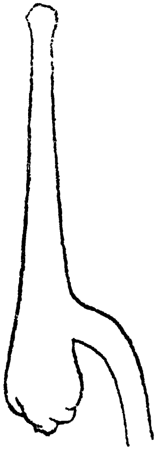
	No. 1.	*No.* 2.
Total length	936	1700 (5 ft. 8 in.).
Arms, length L1	760	—
2	550	—
3	600	—
4	550+	—
R1	764	1460
2	650	1490
3	400 (hect.).	820 (hect.).
4	530+	1255
Web, arms 1–1	143	—
1–2	138	214
2–3	115	—
3–4	110	195
4–4	90	106
Mantle, breadth per cent. length	39	49
Head, breadth per cent. mantle-length.	26	35
Diameter of the largest sucker (as per cent. mantle-length)	10	15
Length of hectocotylus (as per cent. mantle-length)	6·2	8·0

Text figure 3.



Macroctopus maorum. Hectocotylus.

Text-figure 4.



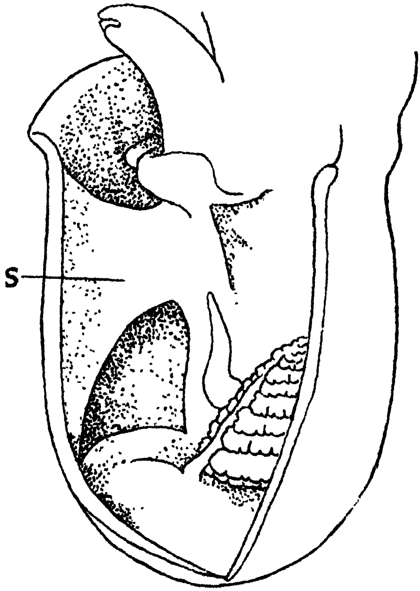
Macroctopus maorum Penis.

2. On the Subdivision of the Mantle-cavity in *Macroctopus*.

In the Octopoda the ventral portion of the mantle is joined to the visceral mass in the mid-ventral line by a median pallial adductor muscle which arises from the inner surface of the mantle and is inserted into the visceral mass just below the anus.

As I have recently pointed out (1927, p. 260), this muscular sheet divides the mantle-cavity into a right and left cavity, and these are in communication with each other, as the septum formed by the median adductor is incomplete towards the apex of the mantle. In preparing the short note alluded to above, I felt very uncertain as to whether the septum formed by the adductor and the subdivision of the mantle-cavity had any functional significance in itself and apart from the presence of the adductor muscle. It seemed quite likely that the actual division of the mantle-cavity was fortuitous, though I pointed out that the septum was in certain forms very extensive and was formed, not only by the muscle in question, but also by additional sheets of connective tissue. In the course of an investigation of *Macroctopus maorum* I have discovered in the latter a very remarkable modification of the septum which merits description.

Text-figure 5.

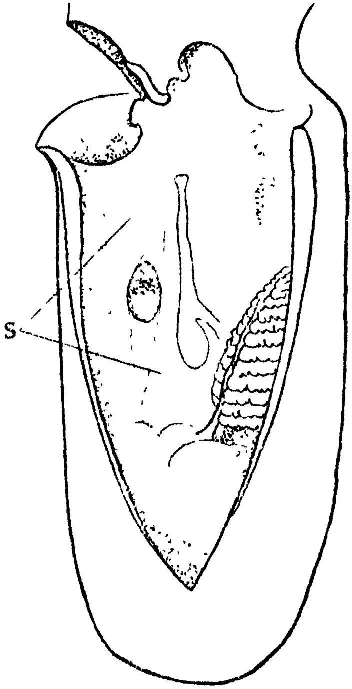


Mantle-cavity of *Octopus vulgaris*. S. Septum formed by adductor muscle.

In *Octopus vulgaris, rugosus*, and, in fact, in nearly all the forms of which I have examined the septum in detail, the latter assumes the form seen in text-fig. 5. The adductor is inserted along the mid-ventral line of the inner surface of the mantle-cavity. For a considerable part of its extent its fibres lie parallel to the mantle-wall. Towards the anterior end of the latter they dip downwards, and are inserted over a fairly broad area of the surface of the visceral mass, apparently into the fascia that surrounds the depressor siphonis muscle on each side. The right and left parts of the mantle-cavity thus incompletely separated are in communication through a large orifice which is bounded above and anteriorly by the adductor muscle, posteriorly and below by the adjacent viscera (kidney, gonad, etc.).

In *M. maorum* (text-fig. 6) a very different state of affairs is found. The septum is very extensive and the orifice leading from one side of the mantle-cavity to the other is very small, nor is it bounded by the same organs as in *O. vulgaris*. Anteriorly and above it is, as in *vulgaris*, bounded by the adductor; but its inferior and posterior edges are composed of entirely new structural elements. There is developed a longitudinal band of muscle which seems to be a branch of the adductor, though it obviously does not share in the function of that muscle. This forms a ventral and posterior partition of considerable extent which is absent in *O. vulgaris* and its allies. Sheets of connective tissue further contribute to the area of the septum and

Text-figure 6



Macroctopus maorum. S. Septum.

the restriction of the orifice. The net result is that the mantle-cavity is divided into two by a very well-developed septum, and the communication between the right and left parts is very much reduced. The only other example of this extension of the septum which I can find is in an example of *Enteroctopus megalocyathus*. Whether this division of the mantle-cavity has any special significance must remain uncertain. It may be purely secondary and the result of the development of the adductor muscle. In *Macroctopus maorum*, however, the septum is so large, and its increase is due to structural novelties that do not seem to be concerned in the original functions of the adductor, that I am inclined to think that it has some special use or significance. In *Macroctopus maorum* the structure of the funnel and the architecture of the mantle-aperture are strikingly different from that of *O. vulgaris*. In particular, it is to be noted that the locking-ridge is very well developed in *vulgaris* and is very weak and almost absent in *maorum*. The general impression obtained from a comparison of the two forms is of a very radical difference in the function of the mantle and its derivatives as a pumping and locomotor organ. It should be pointed out that *Macroctopus maorum* is a very narrowly-built form and very unlike the rather squat *O. vulgaris*.

3. BIBLIOGRAPHY.

HUTTON, F. 1880. Manual of the New Zealand Mollusca, p 1.
——, 1882. Trans. New Zealand Inst. xiv. p. 162.
— . 1904. Index Faunæ Nov. Zelandiæ, p. 57.
PARKER, T. 1885. 'Nature,' xxxii. p. 586.
FILHOL, R. 1885. Mission de l'isle Campbell. Mollusques, iii. 2 p 517.
ROBSON, G. C. 1925. Journ. Linn. Soc., Zool. xxxvi. p. 99.
——. 1926. Proc. Zool. Soc. p. 1323.
- —. 1927. Ann. & Mag Nat. Hist. (9) xx. p. 219
SUTER, H. 1913. Manual of the New Zealand Mollusca, p 1061.

EXHIBITIONS AND NOTICES.

February 7th, 1928.

Prof. J. P. Hill, F.R.S., Vice-President,
in the Chair.

The Secretary read the following Report on the Additions to the Society's Menagerie during the months of October, November, December, 1927, and January, 1928:—

October.

The registered additions to the Society's Menagerie during the month of October were 215 in number. Of these 63 were acquired by presentation, 55 were purchased, 4 were deposited, and 93 were born in the Menagerie.

The following may be specially mentioned:—

2 Brown Tree-Kangaroos (*Dendrolagus inustus*), from New Guinea, purchased on October 6th.

3 Javan Swine (*Sus vittatus*), presented by Mr. F. Shaw Mayer on October 6th.

2 Pluto Monkeys (*Cercopithecus leucampyx*), from Benguela, presented by Messrs. Thomaz de Camara and T. A. Barns on October 9th.

3 Long-eared Foxes (*Otocyon megalotis*), from East Africa, purchased on October 19th.

2 Brindled Gnus (*Gorgon taurinus*), from South Africa, purchased on October 29th.

November.

The registered additions to the Society's Menagerie during the month of November were 88 in number. Of these 37 were acquired by presentation, 33 were purchased, 12 were deposited, 2 were received in exchange, and 4 were born in the Menagerie.

The following may be specially mentioned:—

2 young Koalas (*Phascolarctos cinereus*), from Queensland, purchased on November 10th.

1 Lion cub (*Felis leo*), born in the Gardens on November 13th.

2 Stanley Cranes (*Tetrapteryx paradisea*), from South Africa, purchased on November 21st.

1 Red-faced Barbet (*Lybius abyssinicus*), from Abyssinia, new to the Collection, received in exchange on November 29th.

DECEMBER.

The registered additions to the Society's Menagerie during the month of December were 107 in number. Of these 67 were acquired by presentation, 16 were purchased, 12 were deposited, and 12 were born in the Menagerie.

The following may be specially mentioned:—

2 Chinese Crow-Tits (*Suthora webbiana*), new to the Collection, presented by H. C. Eustace, Esq., on December 13th.

A valuable collection, from Portuguese East Africa, consisting of 1 Red-headed Squirrel (*Funisciurus palliatus*), 4 White-winged Lagwings, and a number of other birds, new to the Collection, presented by J. Spedan Lewis, Esq., F.Z.S., on December 26th.

JANUARY, 1928.

The registered additions to the Society's Menagerie during the month of January were 115 in number. Of these 29 were acquired by presentation, 58 were purchased, 19 were deposited, 6 were received in exchange, and 3 were born in the Menagerie.

The following may be specially mentioned:—

A family of Orang-Utans (*Simia satyrus*), consisting of an adult male, a female, and a young one from Sumatra, purchased on January 21st. 2 Thomas's Langurs (*Presbytes thomasi*), from Sumatra, new to the Collection, purchased on January 21st.

Mr. D. **SETH-SMITH**, F.Z.S., exhibited a living example of a blue variety of a Masked Lovebird (*Agapornis personata*) from Tanganyika Territory. The plumage was blue and white where it would be green and yellow in the normal bird, while the bill was flesh-coloured and the feet grey. This interesting bird had been acquired by the Society from Mr. G. B. Chapman, the well-known animal dealer, who had imported it.

Mr. Seth-Smith also exhibited the skin of an abnormal specimen of the Gouldian Grassfinch (*Poëphila gouldiæ*). which showed gynandromorph characters. The right side was typical of the male of the red-headed (*mirabilis*) phase, while the left side was that of a typical female with black face showing slight traces of red.

This bird had been kept in captivity by Mr. S. Harvey, of Adelaide, South Australia, who, upon its death, had presented it to the Adelaide Museum, the authorities of which had, however, allowed it to be sent to England for inspection. Mr. Harvey stated that it had actually produced eggs, but these had proved to be infertile.

Major S. S. Flower, O.B.E., F.Z.S., exhibited three photographs taken by Mr. Geoffrey C. Flower in the Red Sea. Two were of a young Arabian Gazelle (*Gazella arabica*), from Farsān Island, the type-locality of the species; and one of a Flat-Lobster, *Scyllarus* sp., which had weighed about 3½ lbs.

February 21st, 1928.

Major S. S. Flower, O.B.E., Vice-President,
in the Chair.

Dr. G. M. Vevers, F.Z.S., and Mr. L. C. Bushby, F.E.S., exhibited, and made remarks upon, specimens of the Mitten Crab (*Eriocheir japonicum*).

The Hon. Ivor Montagu, F.Z.S., exhibited, and made remarks upon, a series of photographs taken during a recent visit to the Moscow Zoological Gardens.

Mr. G. C. Robson, M.A., F.Z.S., exhibited a series of lantern-slides illustrating his remarks upon "Some Observations on the Oviposition of *Octopus*."

March 6th, 1928.

Prof. E. W. MacBride, F.R.S., Vice-President,
in the Chair.

The Secretary communicated the following "Note on Uganda Gorillas," by C. W. Chorley, F.Z.S.:—

NOTE ON UGANDA GORILLAS SEEN DURING A VISIT TO MOUNT SABINIO. CHRISTMAS, 1927.

A short note on my trip to Mount Sabinio, the hardest of all the mountains to negotiate, may be of interest. The weather was bad—rain and cold and two days, the balance of five days' hard travelling, were spent on the Ridge.

On Mount Sabinio gorillas have a naturally protected reserve from man, formed by the exceedingly dense undergrowth, through which one literally has to hack one's way. In the upper Bamboo Zone only a few specimens were seen. They were feeding among the bamboos, and occasionally I had a glimpse of two young gorillas who seemed bent on mischief, for, instead of picking off and eating the young shoots as their elders did, they deliberately climbed the bamboos until the stems bent beneath their weight, when they would break off and throw away the few inches from the top of the stem.

The old male would be seen at the head of the family party, occasionally walking a little way in an erect position with a peculiarly human gait, while his wives, four in number, followed with two young ones that were just like little balls of black fluff. The old grey-backed male seemed to have a surly temper, for sometimes he would grab one of his wives by the head and succeed in throwing her ten yards away. Nevertheless, his wives appeared to regard him with real affection, and drove away two males who came too near. My curiosity nearly led me into trouble, for, on approaching nearer to the family party, one of the females charged straight at me, but by shouting I was able to frighten her off. I feel sure that this attack was not accidental, for, as a rule, they only charged when disturbed several times. The male gave his hellish challenge as they left for the upper ridge of the mountain.

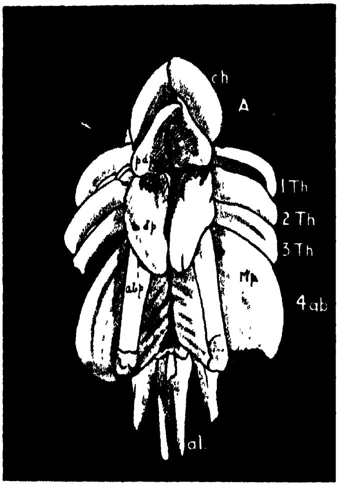
On the second day I approached them high up on the same ridge, and this gave me an opportunity of observing a female who was carrying a restless infant. Sometimes it would be upside down, grasping its parent's hair with its hind legs, while at other times it would get round the back of the neck of its mother, who would then grab it by the hair of its head.

I could not say if the gorillas had increased in numbers since my previous visits. No leopards were seen, but their pug-marks were noted in several places.

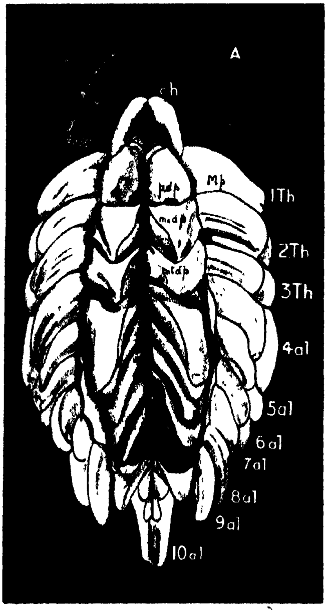
Photography was out of the question owing to the weather, but I have some good photographs of their sleeping-places, also one of a nest about 6 feet high.

Mr. F. Martin Duncan, F.Z.S., exhibited, and made remarks upon, a series of Cinematograph Films taken in the Society's Gardens.

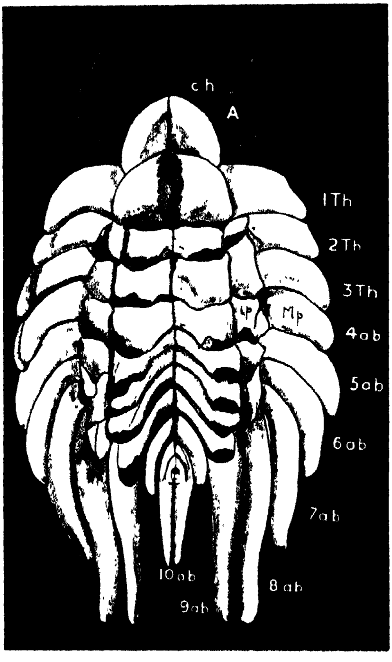
['Proceedings,' 1927, Part IV. (pp. 797–1009), was published on January 12th, 1928.]


ch
A
pd
1Th
2Th
3Th
dp
abp
Mp
4ab
al.

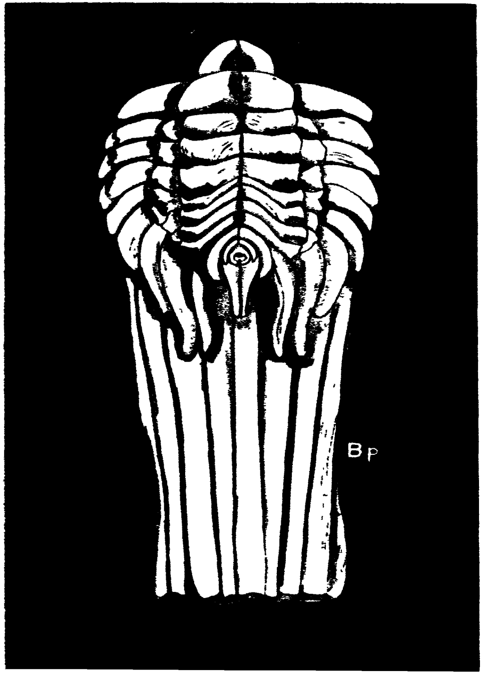
1

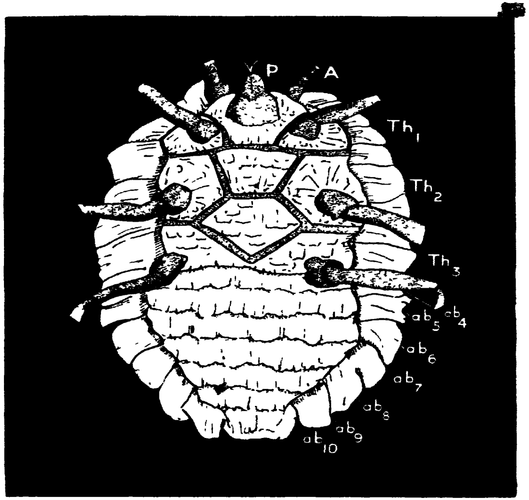

A
ch
pdp
Mp
1Th
mdp
2Th
mtdp
3Th
4al
5al
6al
7al
8al
9al
10al

2


ch
A
1Th
2Th
3Th
Lp
Mp
4ab
5ab
6ab
7ab
10ab
8ab
9ab

3





5

14. The External Morphology and Life-history of the Coccid Bug, *Orthezia urticæ* Linn. By ENID K. SIKES, B.Sc., The University of Birmingham*.

[Received November 2, 1927: Read March 6, 1928.]

(Plates I. & II.†; Text-figures 1–23.)

CONTENTS.

	Page
Introduction and Historical	269
Methods	270
Specific Features	272
External Morphology	272
(*a*) Larval Instars 1 and 2	272
(*b*) Female Instars 3 and 4	286
(*c*) Male Instars 3, 4, and 5	290
Life-history	297
(*a*) Habits of the Larva	297
(*b*) Habits of the Female	299
(*c*) Habits of the Male	300
Summary	302
Literature References	304
Lettering of Figures	305
Explanation of the Plates	305

INTRODUCTION AND HISTORICAL.

The investigation upon the Coccid bug, *Orthezia urticæ* Linn., was carried out between 1925 and 1927, which time allowed for the observation of the complete life-cycle of the insect.

So far as I have ascertained from available literature, no complete account of the anatomy of this species has been recorded, and only vague references have been made to the number of instars in this and closely-related members of the Coccidæ.

As very few males occur each year, it was not possible to describe them in so much detail as the females.

A paper on the internal anatomy of the larva is almost complete.

The pterygote insects are divided into two groups—the Exopterygota and the Endopterygota. The Exopterygota pass through a simple metamorphosis, rarely accompanied by a pupal instar. The wings develop externally and the young are generally nymphs, which possess mouth-parts similar to the adult and functional compound eyes. The Endopterygota pass through a complex metamorphosis accompanied by a pupal instar. The wings develop internally as imaginal discs in the larva. The larva differs in form from the adult, and the mouth-parts are constructed differently. The eyes of the larva are simple, or, if compound, they are non-functional. The Hemiptera are classed with the Exopterygota. It seems, however, that in *O. urticæ* we have an insect in which the female is a degenerate wingless Exopterygote, although the simple eyes indicate alliance with larvæ of the Endopterygota. The male is definitely an Endopterygote insect, having a complex metamorphosis. The larva bears simple eyes, has imaginal wing-buds, and two pupal instars are present in its life-history, although the "pupa" resembles an Exopterygote nymph. It appears, therefore, that *O. urticæ* is an intermediate form of insect connecting the Exopterygota with the Endopterygota. Carpenter (**6**) records the occurrence of imaginal discs among some Coccidæ and Aleyrodidæ.

---

* Communicated by H. G. NEWTH, F.Z.S.
† For explanation of the Plates, see p. 305.

Before 1880 it seems probable that many authors confused the two species, *O. urticæ* and *O. cataphracta*. Douglas (**10**), however, in 1880 described the external features by which these two species could be distinguished. According to this author the first reference to *O. urticæ* was in 1730 by Frisch (**17**).

The species has also been mentioned by Linné (**26**) (1767) as *Aphis urticæ*; De Geer (**8**) (1778) as *Coccus floccosus*; Fabricius (**15**) (1794) as *Coccus dubius*; Bosc (**4**) (1784) as *Orthezia characias*; l'Abbé d'Orthez (**9**) (1785) as *Dorthezia characias*; Latreille, Burmeister (**5**) (1835), and Zetterstedt (**34**) (1840) as *Dorthezia urticæ*; and Westwood (**32**) (1840) as *Dorthezia characias*. In 1843 Amyot and Serville (**1**) restored the original name of *Orthezia* in accordance with its derivation.

I have been unable to procure the paper by Signoret (**31**) (1875) on *O. urticæ*.

Some of the descriptions by List (**25**) (1887) on *O. cataphracta* hold for the species *O. urticæ*.

Newstead (**28**) (1902) briefly described the external anatomy of this species. Kirchner's (**24**) (1912) description of *O. urticæ* is the most complete account dealing also with the life-history.

Fabre (**14**) deeribes the life-history of *O. urticæ*, and Schmidt (**30**) may also be mentioned, as his descriptions of the Coccid, *Aspidiotus nerii*, show analogies to *O. urticæ*.

The investigation of *O. urticæ* was commenced under the supervision of the late Professor F. W. Gamble, F.R.S., to whom I am indebted for assistance during the early part of the work. I wish to express my indebtedness to Mr. L. Eastham, M.Sc., for his help and encouragement during the whole of my work, and for obtaining for me my first supplies of material. To Mr. H. G. Newth also I express my thanks for helpful advice in technique.

METHODS.

The majority of Coccids were collected at Wood End, about 10 miles south of Birmingham, where a colony was found on the south bank at the side of a quiet road. They occurred most extensively in sheltered parts where the undergrowth was thick, in the vicinity of a wooded copse and always on the south bank. The chief vegetation on the bank was Couch-grass (*Agropyrum repens*), Wood-sage (*Teucrium scorodonium*), and Lesser Stitchwort (*Stellaria graminea*).

They have also been found on south banks near Solihull and Barnt Green, both south of Birmingham, but they do not occur in the vicinity of my home, about 15 miles north-east of Birmingham, on banks similarly situated and with the same food-plants growing in abundance.

I have found *O. urticæ* comparatively easy to rear under laboratory conditions. They bred extensively during the summer months of 1926; so that from 60 put in the breeding-cages, under observation, at the beginning of the year, I had between 400 and 500 individuals in all stages of development by August 1926, apart from many fixed or dissected for investigation during those months.

In the breeding-cages I gave the Coccids the three chief plants that I found them on at Wood End, but it was noticeable that they avoided the Agropyrum and fed only on the Teucrium and Stellaria. The best method for breeding the Coccids in the laboratory is to keep them on cut pieces of the food-plant placed in low dishes of water surrounded by dead leaves, moss, twigs, etc., frequently changing the plants for fresh pieces. I tried planting the sage in flower-pots in the laboratory, but it did not prove such a satisfactory method.

In winter the Coccids were found low down in the bank among the dead leaves and undergrowth. Some were allowed to hibernate in this way in the laboratory by putting earth and dead leaves etc. in a zinc tray. Others were kept in the warmth and supplied with fresh food throughout the winter. Artificial light was often directed on these during the daytime. They kept moderately active and fed throughout the winter. The males metamorphosed earlier than those in the natural state.

To ascertain the number of instars, one or two females bearing brood-sacs were put on sage under separate glass cylinders covered with bolting-silk. When the young larvæ emerged from the brood-sac, I distributed them among other cylinders, never putting more than six of the larvæ under one cylinder, so that each could be observed daily. After ecdysis took place, the larvæ were transferred to a fresh cylinder marked "second instar." After another moult they were again moved to a third cylinder, and so on until the adult stage was reached. Several such series were carried out simultaneously and at different times in the spring and summer months, the result being described below.

The investigation of the external anatomy was carried out by examination of the living insect under the binocular microscope and by making whole mounts of the insect. The Coccid was first deprived of the wax secretion by removal with a needle or by dissolving it in a drop of chloroform. It was then macerated for a short time in gently boiling 10-per-cent. potash. The chitin was stained in some cases with a drop of picric acid in the clearing reagent, or with Congo red. Whole mounts of the proboscis, anal plate, etc., were also made in this way.

The type of locality given above agrees with that mentioned by Newstead (**28**). Green (**19**) gives the same food-plants for *9. urticæ* : namely, *Teucrium scorodonium* and *Stellaria graminia*. Other food-plants from which this species is recorded are *Stellarea holostea*, *Statice armenia* and *S. lemonum*, *Euphorbia characias* and *E. pillosella*, *Armenia maritima*, *Taraxacum*, *Urticaria*, *Ribes* (currant), *Geranium robertianum*, *Trifolium medium*, *Saxifrage*, and *Vicia angustifolia*.

SPECIFIC FEATURES.

The Homopterous Coccid bug, *Orthezia urticæ*, belongs to the subfamily Ortheziinæ, and can be distinguished from *Newsteadia* by the fact that the antennæ of the larvæ have six segments, while those of the larvæ of *Newsteadia* have only four segments.

Newstead (**37**) distinguishes *O. urticæ* from the closely-allied species, *O. cataphracta* and *O. insignis*, as follows :—

A. Dorsal surface of female wholly covered by lamellæ.	
(*a*) Thoracic segments each with a median wedge-shaped lamella. Marsupium short. Dorsal surface flat ...	CATAPHRACTA.
(*b*) Thoracic segments without median wedge-shaped lamellæ. Marsupium long. Dorsal surface not flat.	URTICÆ.
B. Dorsal surface of the female partly naked	INSIGNIS.

Dufour (**12**) agreed with Latreille in not allying *Orthezia* to the Coccids. He called them an isolated group of the family Psyllidæ, the one-jointed tarsus with a single claw agreeing with Coccidæ, but the character of the antennæ, the so-called "beak" lying between the anterior legs, the immobility of the females, the absence of considerable mutations of form placed them far distant from Coccids and nearer Psyllids. By their viscera and development of the hepatic organs, however, *Orthezia* were regarded as being more specialised than Psyllids.

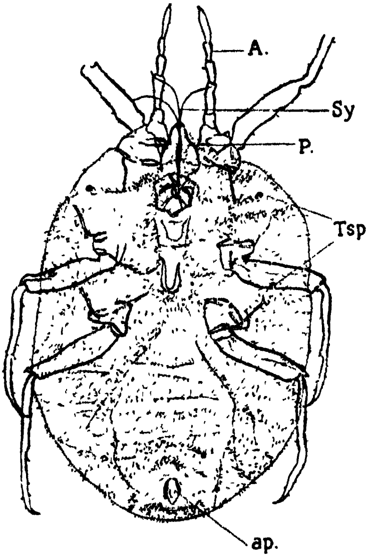
EXTERNAL MORPHOLOGY.

(a) LARVAL INSTARS 1 AND 2.

The larvæ and adult females of *Orthezia urticæ* are entirely enveloped, except for their legs, antennæ, and proboscis, by a pure white secretion. It is a product of the hypodermal cells, some of which are modified as large gland-cells which pour their secretion on to the external cuticle through chitinous spines (text-fig. 12, *g.s.*). These cover the surface of the body and act as glandular ducts. The separate wax filaments thus formed fuse together as wax plates or lamellæ, which assume grotesque shapes, giving the insect a beautiful appearance. The arrangement of these wax lamellæ is constant for each larval instar. The younger the instar the more fused, and therefore more simple, is the arrangement of the wax plates (Pl. I. figs. 1–3, Pl. II. fig. 4).

The wax secretion is soluble with difficulty in boiling water or hot alcohol. It is easily soluble in boiling benzol and in chloroform or glacial acetic acid. Von Fürth (**18**) also finds it soluble in ether or acetone, and says that it crystallises in the cold as needle-like lamellæ. Amyot and Serville (**1**) call the wax "a substance like starch," which describes its appearance but not its composition. Kirchner (**24**) says that Signoret (**31**) mistook the "cereous matter" for "calcareous matter."

Text-figure 1.



Second instar larva with wax removed. Male. Ventral view, × 102. Camera. Comp. Ok. 12, Obj. Leitz 1. (For explanation of letters, see p. 305.)

According to Von Fürth (**18**) the wax of Coccids has been made use of as an article of commerce since the thirteenth century. He said that cerotic acid and its alcohol are combined together in the wax of *Orthezia* as a kind of ester.

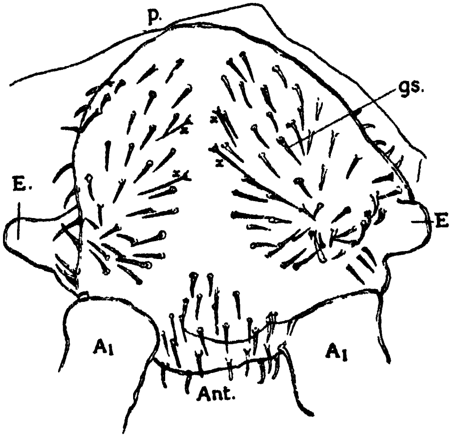
According to Winterstein (**33**) the waxy substance produced by *O. urticæ* and other indigenous larvæ of Hemiptera is an ester of cocceryl acid, $C_{31}H_{62}O_3$, and cocceryl alcohol, $C_{30}H_{62}O_2$. He gives Liebermann's method for their separation and purification.

He also quotes Raimann in saying that wax near the Coccid integument contains also a number of ether-soluble fat constituents, mainly myristic acid and glycerine ester.

The First Instar Larvæ. (Pl. I. fig. 1; text-figs. 1-11.)

The first instar larvæ are greenish or pale brown when taken from the brood-sac and are mite-like creatures. The wax they possess on emerging is arranged in four longitudinal rows on the dorsal surface, the ventral side still being bare. After three days the dorsal surface has attained the grotesque appearance shown in Pl. I. fig. 1. The colour of the integument beneath the wax has darkened considerably. The dorsal wax plates are larger, in proportion to the size of the insect, in the first instar than in later instars.

Text-figure 2.



Head of first instar larva. Dorsal view. Camera. Comp. Ok. 8, Obj. Zeiss D.
(For explanation of letters, see p. 305.)

The head bears a pair of wax horns (Pl. I. fig. 1, *Ch.*) which bend forwards, upwards, and converge towards each other over the bases of the antennæ (*A.*) with a slight torsion. The prothoracic dorsal wax plates (Pl. I. fig. 1, *pdp.*) are blunt triangular pyramids, also converging and pointing slightly forward. The meso- and metathoracic plates are fused, forming a pair of large blunt horns (Pl. I. fig. 1, *mdp.*) pointing towards the hind end. There is also a marginal plate, concave posteriorly, projecting from the side of each thoracic segment.

The wax secretions of the first six abdominal segments are fused, forming two large blocks (*abp.*) which diverge from the median line of the insect and, inclining backwards, end in a blunt point which lies approximately over the last segment of the insect. These median abdominal blocks have very definite angles at the borders of their surfaces.

The marginal wax plates of the first five abdominal segments are also fused, forming an almost semicircular block on either side, cut off like a wedge posteriorly. Indications of segmentation in the block can be seen showing connection with the abdominal segments. The sixth abdominal marginal plate projects freely backwards in a line with the median abdominal wax blocks. The seventh or anal segment has a small wax tube (*al.*) pointing upwards and slightly backwards so that the "honeydew" (see p. 298) is cast away from the surface of the white wax armour. The marginal plates of this segment are small scales close to the base of the tube, surrounding it antero-laterally. From the sides of the anal segment a long plate stretches back posteriorly and divides one-third of its length from the origin, and, in larger specimens of this instar, meets again at the end.

The ventral surface is covered with small wax flakes lying flat on the body, those of an anterior segment overlapping those of the segment behind like tiles of a roof (Pl. II. fig. 5). When the wax is removed, by dissolving it in chloroform, the larva appears cylindrical or oval.

The larva has ten segments behind the head. The lines of demarcation and divisions of the body are fairly distinct in the abdomen (text-fig. 1). The division between head and thorax, and thorax and abdomen, are not so clear, for there is no constriction, the contour of the whole insect being fairly even.

The length of a larva taken from a brood-sac when just hatched is, on the average, 0·440 mm. long by 0·314 mm. at the widest part, which is at the first abdominal segment. When they emerge from the brood-sac they have attained an average length of 0·530 mm. by 0·390 mm.

The length of the head is one-fourth the length of the whole body, the thorax one-third of the whole insect.

The metathoracic legs, without the claw, are the same length as the whole insect, the prothoracic legs are slightly longer than the body, and the middle or mesothoracic pair are slightly longer still. It is the tibial portion which differs in length, as the coxæ and femora of all three pairs are equal in length.

The antennæ (*A.*), consisting of six segments, arise from the anterior border of the head, each at its base being one-third the width of the head. The antenna is two-thirds the length of the body from its junction to the end of the distal spine.

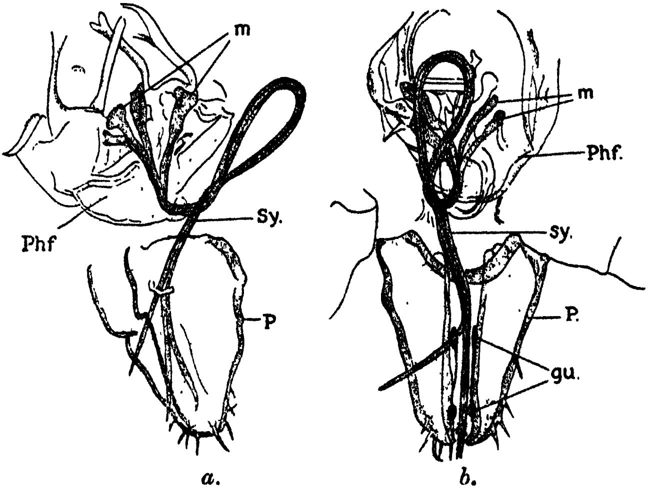
There is a pair of simple eyes (text-fig. 2, *E.*) in each larval instar, each situated on the dorsal surface of the head and lateral to, and slightly posterior to, the antennæ, projecting antero-laterally from the head. The eye is conical in shape, and in the first and second instars has a minute pimple on the lower part of the side facing the antenna.

The proboscis is cone-shaped, and large in proportion to the size of the insect, being five-sixths the length of the head or nearly one-fourth the length of the whole larva. At its proximal end the proboscis is almost as broad as it is long, and at the distal end one-third the width of the head.

The function of the head-capsule is not so much to protect the underlying organs as it is to give support to the structures connected with piercing and suction, and its ventral surface to give attachment to the muscles controlling the pharyngeal framework.

The proboscis or rostrum of the larva is composed of extremely hard chitin and is a very dark brown colour. It projects ventrally from the head and comes to lie between the first pair of legs (Pl. II. fig. 5). At the distal end of the proboscis are about ten long setæ (text-fig. 3 *a* and *b*) which are sensory in function. The proboscis is composed of one segment only, as opposed to the multi-segmented proboscis of some Homoptera.

Text-figure 3.



Proboscis of larva, whole mount. Camera. Comp. Ok. 12, Obj. Zeiss A.
(For explanation of letters, see p. 305.)

The mouth-parts are adapted for piercing and sucking, the food being entirely fluid. The rostrum, which is a modified labium, is grooved along its anterior surface to form a deep channel in which lie the piercing stylets (text-fig. 3 *a* and *b*). In the groove on either side of the stylets are two pairs of darkly-staining bodies, probably gustatory organs (*gu.*, text-fig. 3 *b*).

There are four stylets which are slender and bristle-like, and represent a pair of maxillæ and a pair of mandibles. These are extremely long, and, when drawn in, are looped back into a chitinous pocket (text-fig. 3) which runs backwards and slightly upwards and lies ventral to the nervous system. The mandibles are external to the maxillæ, and the latter appear as a single grooved stylet because they lie very close together. The internal ends of the stylets are slightly broader, and are connected to strong muscles inserted in the pharyngeal framework.

The ventral surface of the head is almost entirely occupied by the base of the proboscis. The eyes (*E.*) project laterally one-fourth the width of the head-capsule, which is slightly shorter than it is broad. The head is attached to the first thoracic segment by a less chitinised region, so that a certain amount of movement may be possible, but is not apparent.

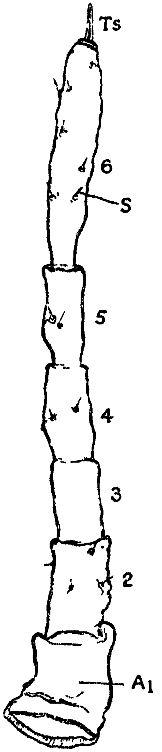
The dorsal capsule of the head (text-fig. 2) is roughly rectangular, with the posterior corners rounded and a pointed projection between the antennæ which becomes rounded in older larvæ. The dorsal surface is covered with glandular setæ. The proboscis is usually extended forward in such a way that the head-capsule overlies the ventral part of the prothorax and junction of the first pair of legs. The setæ are arranged in three groups on the head-capsule (text-fig. 2). Inspection of the setæ shows that they lie in connection with the cephalic wax "horns" (Pl. 1. fig. 1, *Ch.*). Two groups of about 50 setæ lie dorso-posteriorly to the antennæ and eyes. The apices of the setæ of these groups converge towards a point near the front of the group, causing the pyramidal shape of the horns. Some of the spines on the antero-lateral border of the group are distinctly curved, which fact causes the secreted "horns" to converge anteriorly (text-fig. 2, right group). Four setæ (*x*), differing from the others in that they are longer and more slender, occur constantly in the middle of the head-capsule, one pair on the median border of each group of glandular setæ. Each is set in a cup-like pit with the edges above the surface of the integument. Between the antennæ on the anterior dorsal surface of the head-capsule is another group of secreting setæ, about 26 showing dorsally; but the group stretches to the junction of the proboscis in front, and in all there are 33 anterior setæ.

The antennæ (text-fig. 4) is a darker shade of brown than the body, and is composed of six segments. A few setæ occur on the antennæ, which are shorter and finer than the glandular setæ. As wax is never secreted on the antennæ, these are no doubt sensory and not secretory in function. They are inserted in slight depressions on the surface of the antennal chitin. The setæ on the antennæ are extraordinarily constant in position in all first instar larvæ. The positions are shown in text-fig. 4, the usual number to each segment being:—

Segment	1 (proximal) ...	0 setæ.
,,	2.................	4 ,,
,,	3.................	0 ,,
,,	4.................	2 ,,
,,	5........	2 ,,
,,	6.................	8 setæ and one terminal spine.

The terminal spine is a movable peg in a terminal pocket, and must function as an organ of touch. I have only found slight variations in the above arrangement. The sixth segment is nearly twice as long as the other five, which are almost equal in length and taper to a point from 1 to 5. The antennal setæ, presumably sensory, are more acute than the glandular spines of the body, which are blunt and more uniform in thickness to their extremities.

Text-figure 4.



Text-figure 5.

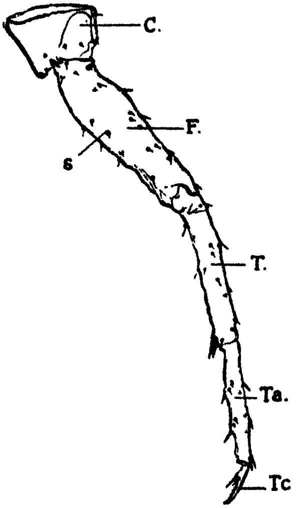
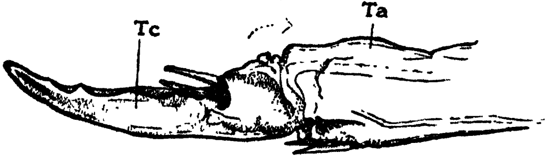


Fig. 4.—Antenna of first instar larva. Camera. Comp. Ok. 8, Obj. Zeiss D.
Fig. 5.—Leg, left prothoracic, first instar larva. Camera. Comp. Ok. 2, Zeiss D.
(For explanation of letters, see p. 305.)

The thoracic segments are broad and strong to contain the muscles of the legs. Their integument is covered with secretory setæ fairly evenly distributed over the surface on the ventral side and inclined posteriorly. On the dorsal side they are arranged in definite median and lateral groups. The lateral setæ are fairly evenly distributed, while the setæ of the median groups converge towards the median line of the body. The spines of these latter groups in the prothorax bend slightly anteriorly, while those of the meso- and metathorax are inclined posteriorly.

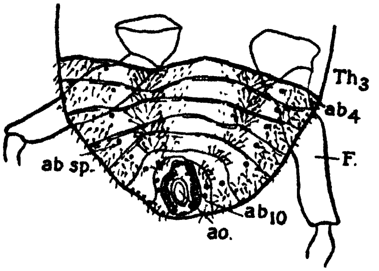
The legs (text-fig. 5) are strongly built, and are inserted deeply in the lateral margin of the body. They are darker brown than the wax-covered parts of the body. They are flattened antero-posteriorly in the walking position. The coxæ (*C.*) are well developed and have six very small setæ (*S.*). There is no

Text-figure 6.



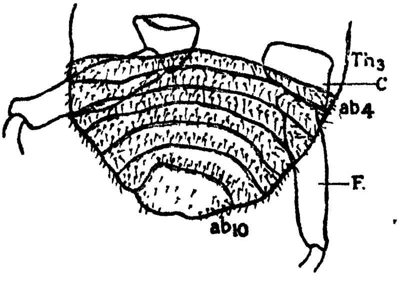
Tarsal claw. First instar. Camera. Comp. Ok. 12, Obj. Zeiss A. (For explanation of letters, see p. 305.)

Text-figure 7.



Arrangement of dorsal abdominal setæ. First instar. Camera Ok. 12, Obj. Zeiss A.
(For explanation of letters, see p. 305.)

Text-figure 8.



Arrangement of ventral abdominal setæ. First instar. Camera. Comp. Ok. 12.
(For explanation of letters, see p. 305.)

sign of trochanters. The femora (*F.*) are about three times as long as broad, and have about 24 small setæ scattered over the surface. The femora (*F.*) are broadest near the body. The tibiæ (*T.*) are about four times as long as they are broad, and the same width all down. They have 15 small setæ, and at the junction of tibia and tarsus a pair of strong ventral spines which lie parallel to one another and make an acute angle with the length of the leg. The tarsus (*Ta.*) consists of a single joint with seven small setæ and four large spines on the surface, and a pair of long, strong, dorsal spines projecting at an angle of 45° at the junction with the claw. The tibio-tarsal joint is fixed. The tarsal claw (*Tc.*) has two ventral spines and is toothed ventrally (text-fig. 6). The ventral side of the claw is concave.

The abdomen consists of seven segments (text-figs. 7 & 8) which are fairly uniform in length, except the anal segment, but decrease in breadth from the first to sixth. Dorsally the anal (seventh) segment is as broad as it is long, and has the anal orifice (text-fig. 9, *ao.*) opening in the middle. In some Coccids, for example in *Aspidiotus nerii*, the anal orifice is ventral. Ventrally the anal segment is about twice as broad as it is long

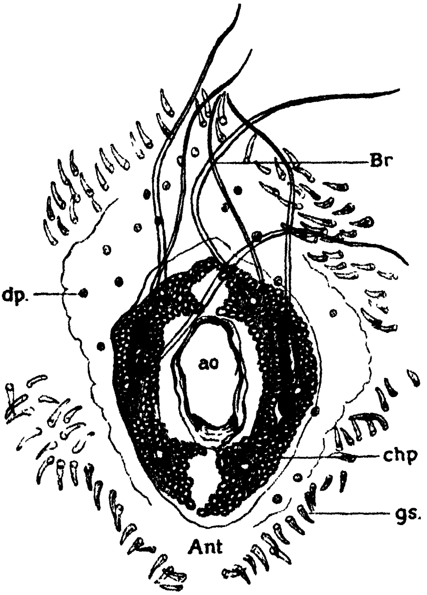
The glandular setæ of the abdomen are distributed on the ventral side (text-fig. 8) in two uneven rows across each segment, the setæ pointing backwards. The lateral setæ are scattered unevenly but thickly over the integument. The dorsal ones (text-fig. 7) are arranged in two antero-posterior rows down the abdomen; the lateral setæ of each of these rows bend in a posterior median direction and the inner spines of the rows bend towards the sides of the insect, showing how the inclined pyramidal wax blocks of the abdomen are formed in such a grotesque shape. The genital aperture is not apparent.

The anal aperture (text-fig. 9) is on the dorso-posterior side of the seventh and last abdominal segment (text-fig. 7). It is an irregularly oval aperture (*ao.*) lying in the middle of a perforated chitinous plate (text-fig. 9, *Ch.p.*). The perforations are the openings of large gland-cells which lie immediately below the plate. There is a longitudinal slit on either side of the anal orifice among the perforations in which the median bristles are inserted. The walls of these slits slope, so that their breadth is greater on the external surface than at the internal surface of the plate. There are six long bristles (*Br.*) arising from the anal plate and inclining posteriorly: they are flexible and hair-like, and each inserted in a little pit between the glandular spaces. They rise up from the anal plate in a dorso-posterior direction, and all converge to a point probably serving the purpose of determining the direction of the anal wax tube mentioned above, which conveys the "honey-dew" away from the surface.

In the larvæ and adult females there are two pairs of thoracic spiracles and eight pairs of abdominal ones.

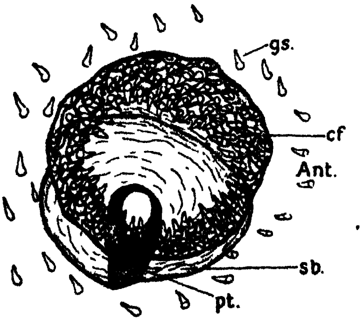
The thoracic spiracles (text-fig. 10) are situated on the meso- and metathorax. They lie on the ventral surface outside the coxæ, the distance from the lateral border being about one-fourth of the width of the thoracic segment. The ventral aperture is strongly chitinised and surrounded by five irregular circles of setæ set in numerous folds of chitin (*c.f.*). The border is simple

Text-figure 9.



Anal orifice. Third instar female. Camera. Comp. Ok. 8, Obj. Leitz 6*a*. (For explanation of letters, see p. 305.)

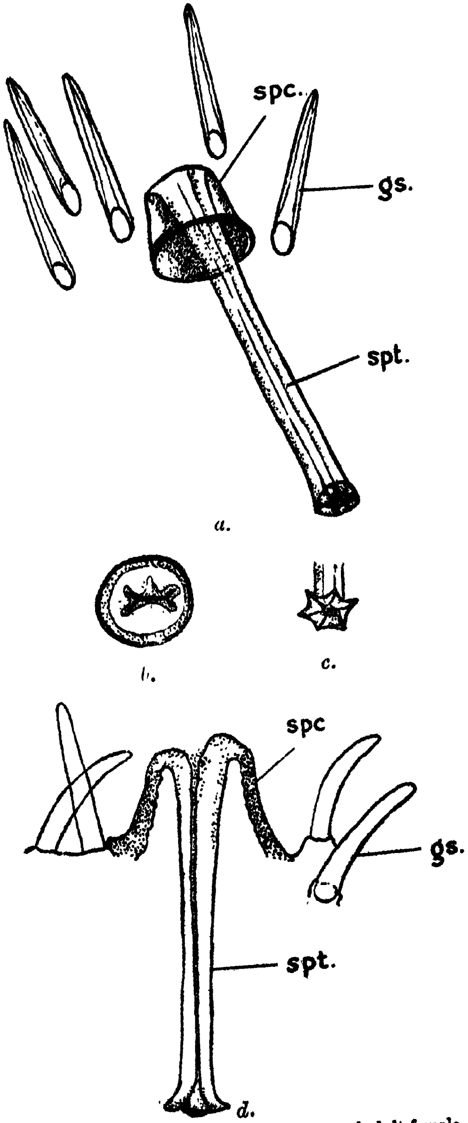
Text-figure 10.



Spiracle. Right metathoracic. Camera. Comp. Ok. 12, Obj. Zeiss D. (For explanation of letters, see p. 305.)

and immobile as in most bugs. The diameter of the surface-opening is 76 μ. They are larger than in *O. cataphracta*, in

Text-figure 11 *a–d*.



Spiracle. Eighth left dorsal abdominal spiracle of adult female. Camera. Comp. Ok. 8, Obj. 1/12 *a*. Oil imm. Leitz.
a. Seen from interior of chitinous integument. *b*. External opening. *c*. Internal opening. *d*. In section.
(For explanation of letters, see p. 305.)

which they have been recorded as having a diameter of 35 μ. The spiracle widens out below the surface into a bulb-shaped swelling (*sb.*) 60 μ in the widest part. Beyond the swelling a short, conical, chitinous tube connects the spiracle with the trachea (text-fig. 10, *pt.*). The dorsal part of this connecting-tube where it joins the trachea is 36 μ in its longest direction, and the ventral opening into the swelling is 18 μ by 12 μ and is pear-shaped. The cavity of the spiracle is directed towards the median line of the insect, the pear-shaped opening being nearest to the coxa.

It seems probable that the bulb and pear-shaped part have some power of opening and closing the tube beneath the spiracle.

Of the eight pairs of abdominal spiracles (text-fig. 7) in *O. urticæ*, one pair is situated in each of abdominal segments 1 to 6, and two pairs in the seventh or anal segment, indicating that this segment is at least two fused segments. The first six pairs lie dorso-laterally on the abdominal segments and about one-third the distance from the anterior to the posterior border of the segment. They are tubular spiracles and much smaller than the ventral thoracic ones. The diameter of the chitinous ring at the opening on the surface of the abdomen is 16 μ.

The tubular part (*sp.t.*) is 40 μ in length (text-fig. 11 *d*). It appears to be striated with six longitudinal ridges running down from a star-shaped opening at the internal end. The surface-opening is a slit in the middle of a circular chitinous ring; the lips of the slit are apparently capable of enlarging the aperture by muscular action (text-fig. 11 *b*). The spiracle opens on the surface as a protruding cone (*spc.*) strongly chitinised, with the tube projecting into it (text-fig. 11 *d*). The internal tube is 6-radiate, and capable of enlarging or closing the connecting apertures (text-figs. 11 *a* & 11 *c*).

The Second Instar Larvæ. (Text-figs. 12 & 13.)

After the first moult, which takes place after two or three weeks in early summer, the second instar larvæ (Pl. I. fig. 2) are about 1 mm. in length by 0·740 mm. in width.

The second instar larva is very similar in appearance to the first. The wax plates are arranged in the same manner, but tend to be split up into a few more plates. Segmental divisions coinciding with the body-segments are still not clear.

With wax removed (text-fig. 1) the insect is now oval or ellipsoidal in outline. The proportions of the parts to one another have changed. The head and thorax are half the length of the whole insect, the abdomen half the length. The antennæ (text-fig. 12) are also half as long as the insect, while the proboscis is much shorter in proportion, being only one-tenth the whole length of the insect. The legs (text-fig. 13) are slightly shorter than the insect, and the metathoracic pair are now the longest. Each leg is approximately the length from the anterior border of the head to the middle of the fifth abdominal segment.

The glandular setæ on the dorsal side of the head are arranged in groups similar to those in the last instar, but the setæ are more numerous. The four median setæ (text-fig. 2, *x*) are still present, but there are others of the same type dotted about among the glandular setæ, approximately five in each dorsal group. Some of the setæ are two and a half times as long as the glandular setæ.

Among the setæ are numerous dermal pores. They are circular plates with four holes in them. In the abdomen they occur chiefly in the intersegmental membranes and on the median axis of the insect between the dorsal group of glandular setæ.

The antennæ (text-fig. 12) are 6-segmented, but the third (*A*. 3) shows a difference from the first instar larvæ, having elongated to about twice the length of the basal or second segment. This point is of interest because the growing region of the antennæ has been shown to be in this segment in dragonfly nymphs (2) in Ephemerids and probably in Pentatomid bugs. The antennal setæ (*S*.) are again extraordinarily constant in number and position (text-fig. 12), the most common number being:—

Segment 1 (proximal)....	1
„ 2.................	2
„ 3.................	3
„ 4.............	2
„ 5.................	3
„ 6.................	8 and one terminal spine.

The positions are as in text-fig. 12.

The thoracic glandular setæ are more numerous, but are grouped as in the first instar.

The setæ on the legs (text-fig. 13) are again fairly constant, and only differ from the setæ found in the first instar in that two of the femoral setæ are differently situated and there are one or two additional large spines on the tarsus. There is also a circular plate-like depression (text-fig. 13, *pd.*) always present at the proximal end of the femur. The claw curves more at its tip than in the first instar.

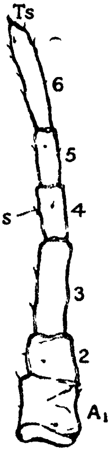
On the seven abdominal segments the setæ are far more numerous. On the ventral surface there are four irregular transverse rows of setæ on each segment, broadening out at the sides into six rows. The setæ are set closer together. On the dorsal surface groups of setæ converge as in the first instar. On the first segment there are eight rows of sixteen setæ in a group of one side. The number of rows of setæ decrease in width, so that the sixth abdominal segment has only four rows of twelve setæ. The dorso-lateral setæ are numerous and closely set, there being about eight rows in the widest part.

One or two of the long pointed setæ (text-fig. 2, *x*) appear among the glandular ones as on the dorsal part of the head, and a pair of these lie in the median line between the two groups of setæ on each segment.

The anal orifice and plate are situated more dorsally than in the last instar, but in appearance are similar.

Kirchner (**24**) described a constriction between thorax and abdomen in newly-hatched larvæ which disappears before the end of the first instar. I could not detect any such constriction. According to List (**25**), Signoret (**31**) recorded seven segments to the antennæ in the first instar larvæ of *O. urticæ*. It seems probable that, if he was dealing with this species, he counted the terminal spine as a segment.

Text-figure 12.



Text-figure 13.

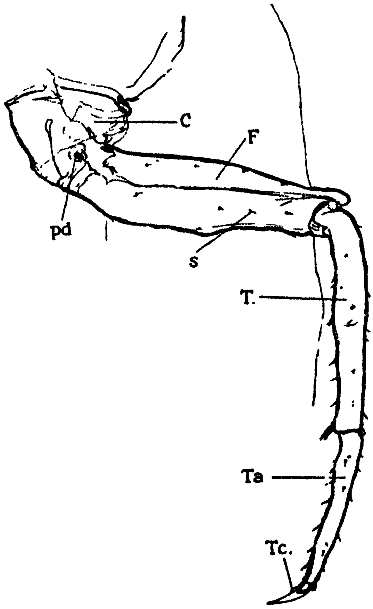


Fig. 12.—Antennæ. Second instar larva. Male. Camera. Comp. Ok. 12, Obj. Zeiss A.

Fig. 13.—Leg. Right mesothoracic second instar larva. Male. Camera. Comp. Ok. 12, Obj. Zeiss A.

(For explanation of letters, see p. 305.)

List (**25**) does not describe separate instars in *O. cataphracta*, but only mentions "young" briefly, and describes the adults in detail. Kirchner's (**24**) "larve mittlerer grosse" corresponds with my second instar larva.

Ferris (**16**) says that abdominal spiracles have been noticed in a limited number of Coccidæ and usually passed over as of no particular significance; regarded as aberrant or only of taxonomic importance.

Mammen (**27**) says that, although the abdominal spiracles are so different from the thoracic ones in some bugs, nevertheless they are physiologically equivalent. He says that in bugs other than *O. urticæ*, in which they occur, the spiracles are in a protective pit and have wider openings. The abdominal spiracles of the closely-allied species *O. cataphracta* are not tubular, but, according to List (**25**) and Newstead (**28**), resemble the thoracic ones.

(b) THE FEMALE INSTARS. (Pl. I. fig. 3, Pl. II. fig. 4; text-figs 14 & 15.)

The Third Instar Female.

The third instar female larva is similar in general appearance to the second, but larger. The length is approximately 2·2 mm. and the width 1·8 mm.

The wax-plates are arranged almost identically with those of the second instar, but are more segmental in arrangement. There are, however, signs of the intermediate blocks (Pl. I. fig. 3, Pl. II. fig. 4, *ip.*) being cut off between the median and marginal blocks on abdominal segments 4, 5, and 6. The marginal plates of abdominal segments 5 and 6 are rather longer, reaching as far posteriorly as the inclined anal tube.

After removing the wax, the dorsal outline of the insect is almost circular and more flattened dorso-ventrally than previously. It is still greenish-brown in colour with dark brown antennæ, proboscis, and legs.

The head and thorax measure three-tenths of the length of the insect, the abdomen seven-tenths. The legs, excluding the claws, are the same length as the body, the metathoracic pair being the longest by a small amount. The antennæ are three-fifths the insect-length and the proboscis one-fifth.

The glandular setæ are more numerous, but arranged similarly to previous instars. The four median long setæ (text-fig. 2, *x*) on the head are still present; they seem to be constant in position in all instars The dermal pores are more numerous on the head than in younger instars.

The antennæ are 7-segmented, segments 3 and 7 are the longest, 1 being very short, wide, and conical, 2 also being short. The antennal setæ are less constant in position than in previous instars, but several antennæ had the following numbers:—

Segments 1–6	3 setæ on each.
Segment 7	6 setæ, and 1 terminal spine.

The dermal pores are extremely numerous in the thorax. On the ventral side they occur in one or two irregular rows, chiefly along the anterior borders of the segmental groups of glandular spines. On the dorsal side, though a few scattered ones appear, they are chiefly found in the median axis of the body in a space devoid of glandular spines between the two median groups, and also sparsely in the intersegmental membranes. These membranes, dorsal and ventral, also exhibit a peculiar sculpturing of the surface in the form of 3-, 4-, and 5-pointed flakes of chitin.

The number and arrangement of abdominal setæ are almost identical with those found in the second instar. The lateral setæ are more numerous in conjunction with the increase in marginal wax plates. In the anal segment the marginal groups meet the central one to form a continuous group of setæ.

On the ventral side of the anal segment can be seen a transverse fold of the integument which marks the genital aperture.

The setæ on the legs are more numerous, and become arranged in regular rows in this and the fourth instar, whereas they were irregularly scattered though constant in position in instars 1 and 2.

The Fourth Instar Female.

The fourth instar (Pl. I. fig. 3, Pl. II. fig. 4) is the adult stage of the female. The size is considerably increased, and different individuals devoid of wax measured from 2·8 mm. to 3 mm. in length by 2·3 mm. to 2·5 mm. in width. The adult female is apterous, and largely resembles the larvæ except in size and later in that it acquires a brood-sac, which doubles its length (Pl. II. fig. 4, *Bp.*).

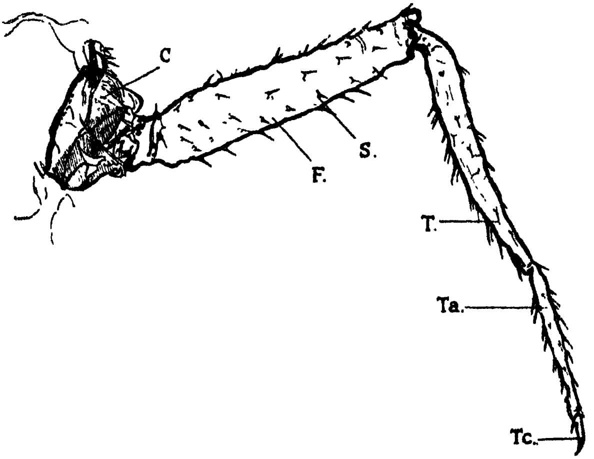
This is the final and sexually adult stage of the female. The wax-plates (Pl. I. fig. 3, Pl. II. fig. 4) have assumed a definite structure coinciding with the segments of the body, and the blocks so formed have smooth surfaces, not grooved as in previous instars. There is no sign of fusion of wax blocks in conjoined segments. The dorsal head wax blocks (*Ch.*) form incurved "horns" as before. The wax blocks of the prothorax are as wide as the cephalic blocks, but the meso- and metathoracic blocks, as well as the first four abdominal ones, cut off small intermediate blocks (*ip.*) laterally between the median and marginal blocks. The marginal wax blocks (*Mp.*) have increased in length, and curve posteriorly and inwards, those of segments 4, 5, and 6 being about twice as long as in instar 2. The plates of the anal form, as before, an anal tube.

The ventral surface is covered with tile-like flakes, as in previous instars. The brood-sac (Pl. II. fig. 4, *Bp.*) begins to form from the ventral surface of the second abdominal segment, and stretches out behind the anal segment until, when full-grown, the insect is twice its normal size. The brood-sac is composed of longitudinal plates above, about seven on the dorsal surface, and the underside is smooth and made up of numerous small plates overlapping slightly like tiles. The brood-sac is completely closed at first; the eggs pass straight into it from the slit-like genital aperture on the ventral side of the seventh segment. When the larvæ emerge from it, the brood-sac splits at the posterior end and later along the sides for a short distance.

The adult female, devoid of wax, appears circular in outline. It is greatly flattened dorso-ventrally, especially in the abdominal region. The proportion of head, thorax, and abdomen to the size of the insect are the same as in the third instar. The ventral abdominal segments 3, 4, 5, and 6 are very much reduced in size and become telescoped into each other, and the abdomen is concave on the ventral surface; the sex-opening is therefore in a deep depression.

The dorsal glandular setæ are very numerous, especially on the lateral borders of the segments connected with the increase in length of the marginal blocks. Their arrangement dorsally is the same as in the third instar. I can detect no break in the sequence of setæ across the segments, which have an intermediate dorsal block. It is, however, noticeable that the setœ at this point of junction of main dorsal and intermediate blocks change their direction and bend away from each other. There is, on the other hand, a definite gap between the setæ which secrete the intermediate blocks and those which secrete the marginal blocks. This suggests strongly that the intermediate blocks really belong to the median dorsal blocks.

Text-figure 14.



Leg. Fourth instar larva. Female. Camera. Comp. Ok. 6, Obj. Zeiss A. (For explanation of letters, see p. 305.)

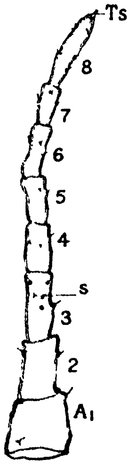
The ventral glandular setæ of the second abdominal segment are extremely numerous in connection with the formation of the brood-sac, and the segment seems to have increased in size as the other abdominal segments decreased. There are at least 23 rows of closely-set setæ, as opposed to 6 or 7 rows on the other abdominal segments. On the ventral side of the anal segment may be seen the short transverse fold of chitinous integument which is the genital aperture.

The legs (text-fig. 14) are about two-thirds the length of the body, the metathoracic legs being slightly longer than the other two pairs. The setæ on the legs are very numerous and arranged in definite longitudinal rows.

The antennæ (text-fig. 15) are 8-segmented. The setæ are less constant than in previous instars. The most common number and arrangement are shown in text-fig. 15.

Segment	1 (proximal).	2 setæ.
,,	2	2 ,,
,,	3	6 ,,
,,	4	3 ,,
,,	5	2 ,,
,,	6	3 ,,
,,	7	3 ,,
,,	8	5 + 1 terminal spine.

Text-figure 15.



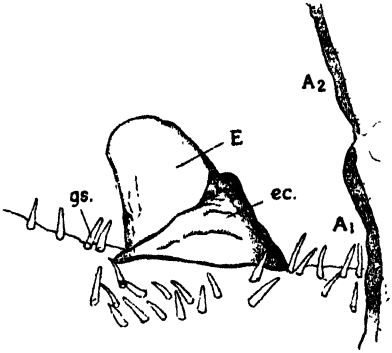
Antenna. Fourth instar larva. Female. Camera. Comp. Ok. 6, Obj. Zeiss A. (For explanation of letters, see p. 305.)

In the third instar female, and even more pronounced in the adult stage, the minute pimple, already mentioned in the larval eye, has become a second more pointed cone (text-fig. 16, *ec.*) projecting from the posterior side of the original protrusion. This is composed of thicker chitin and is of a darker brown colour. The apex of this extra cone is directed inwards and towards the antenna. It projects about half as far from the body-wall as the eye itself. The eye projects 75·0 μ in the adult, and its basal width is 87·5 μ.

It is noticeable that as the insect changes from the first to fourth instar the dorsal surface (after removal of the wax) becomes flatter, until in the adult there is a definite longitudinal depression down the mid-dorsal surface of the insect. In the mature female the anal segment is larger and the anus has become completely dorsal, having gradually, through the different instars, moved from the posterior position found in the first instar. The ventral genital opening has increased in size.

Kircher (**24**) has described the adult wax plates, and my findings agree fairly closely with his. I believe that his abnormal adult females are really third instar females, corresponding with his "Larve mittlere grosse." He does not mention the number of instars, but describes three stages corresponding to the first, third, and fourth instars, a "jüngster stadium" with 6-segmented antennæ, a "Larve mittlere grosse," with 7-segmented antennæ, and finally a "geschlechtsreife Weibchen" with 8-segmented antennæ. Douglas (**11**), Dufour (**12**), and Amyot and Serville (**1**) only describe the adult female. Henneguy (**21**) described briefly the deposition of wax in the adult of *O. insignis*.

Text-figure 16.



Eye. Fourth instar female. Camera. Comp. Ok. 8, Obj. Zeiss D.
(For explanation of letters, see p. 305.)

(b) THE MALE INSTARS. (Text-figs. 17–23.)

The Third Instar Male.

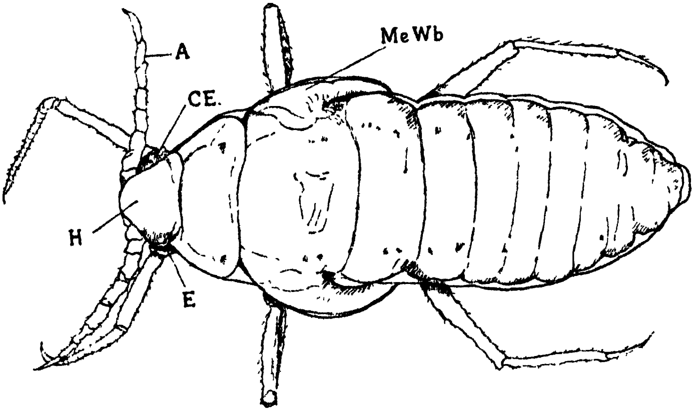
The male nymph of the third instar forms a pure white cocoon. This is composed of loosely-twisted bundles of silken threads and close woolly curls like the wool of sheep. The cocoon is the product of the dermal glands. The silken threads appear first at the junctions of the segments and look exactly like a mould growing on the insect. At the sides of the abdominal segment it grows in tufts, and is more evenly distributed in the middle. Tufts also appear at the junction of the head and thorax. The white threads increase in length and bend forward over the head. The cocoon takes about two days to complete, and then the nymph lies quiescent in it until the next moult. The cast skin of the second instar larva is found at the edge of the cocoon with its wax still adhering to it.

The nymph is cylindrical in shape and pale green in colour. It measures approximately 2·6 mm. in length, but is rather variable. Its general appearance is that of an elongated larva. The body is soft and covered by a transparent cuticle which fits closely on the legs and antennæ.

The antennæ, which protrude from the anterior region of the head at right angles to the long axis of the body, are 8-segmented, wrinkled, and tapering to a point. They measure seven-elevenths the length of the whole insect. The proboscis has disappeared and there is no sign of a mouth, as in the case of the pupæ of some other Coccids.

The segmentation is clearly marked by deep transverse furrows.

Text-figure 17.



Third instar nymph. Male. Dorsal view, × 63. Binocc. Ok. 10, Obj. 32 mm.
(For explanation of letters, see p. 305.)

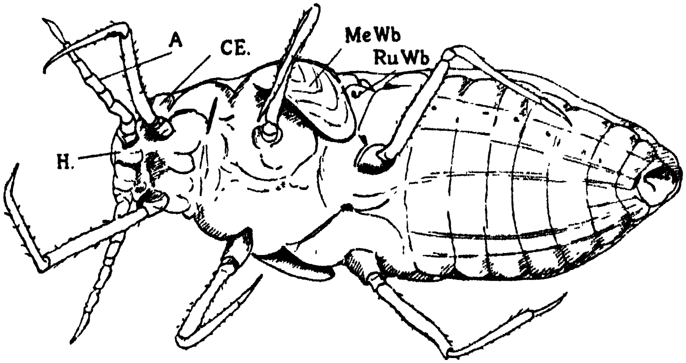
The head and thorax are half the length of the nymph. The head (text-figs. 17 & 18, II.) is distinct from the prothorax and narrower, though there is no "neck." It is triangular from the dorsal aspect. On the sides of the head, posterior to the antennæ, the compound eyes (*CE.*) of the adult appear as rudiments in the form of circular transparent patches of cuticle with a dark anterior region. Over each eye is a transparent protuberance like a minute blister on the outer cuticle, which appears to be the remains of the larval eye, and is probably not functional. The compound eyes are not completely developed and the nymph is most probably blind. The mesothorax is the widest part of the nymph. It bears the external wing-buds (*Me.wb.*) laterally, which bend round and press closely into the sides of the nymph and reach to the middle of the metathoracic segment on the ventral side. The wings are fleshy pads, wrinkled in V-shaped folds under the outer cuticle. The metathorax and following four abdominal segments are almost the same width, being somewhat narrower than the mesothorax.

On the sides of the metathorax can be made out very small buds (*RuWb.*), which are the buds of the future rudimentary metathoracic wings or halteres.

There are eight segments to the abdomen. The last four taper to a downwardly-curved point where the external male genitalia will eventually form. On the dorsal aspect of the eighth abdominal segment can be seen a circular patch in the position of the anal plate of the larva. The anus appears to be abortive in this stage. Six muscle-bands run longitudinally along the abdomen, three on either side.

The legs, which are more slender than those of the larva, measure approximately half the length of the nymph. They bear setæ and have a very small claw at the end of a single-segmented tarsus. The femora have a wrinkled cuticle. The prothoracic legs are the shortest and the metathoracic legs the longest.

Text-figure 18.



Third instar nymph. Male. Ventral view, × 63. Binocc. Ok. 10, Obj. 32 mm. (For explanation of letters, see p. 305.)

Dermal pores have been observed on the cuticle, differing from the larval dermal pores in that they have more and a variable number of loculi in a single plate.

The Fourth Instar Male.

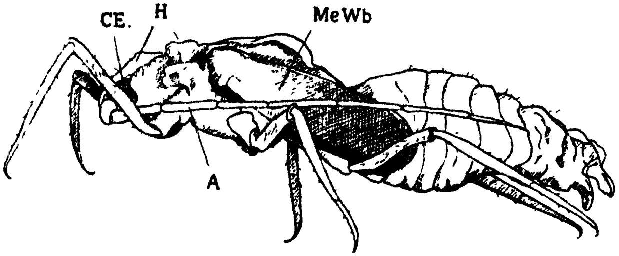
After ecdysis the fourth instar male takes the form of a second nymph (text-figs. 19 & 20). The insect now more closely assumes the shape of the adult. It has shortened considerably, especially in the abdominal region, the length being on the average 2·0 mm. The antennæ (*A.*) lie along the sides of the body and are long and slender, reaching back to the posterior margin of the third abdominal segment. They are composed of nine segments, the two proximal ones being small and the remainder long and slender. They are beset with many setæ and terminate in a strong curved spine.

The segments of the body are clearly marked. The head (*H.*) is distinct from the thorax, there being signs of a neck. A pair of lateral compound eyes (*CE.*), not functional yet, lie behind the antennæ. They are dark red in colour, but lie under the nymphal cuticle.

The head and thorax are now two-thirds the length of the insect. The coxæ of the prothoracic legs are closely applied to each other, the mesothoracic coxæ are lateral and still lie far apart, while the metathoracic coxæ are close together. The legs are two-thirds the length of the whole insect, and are covered with setæ.

The mesothoracic wing-buds are dark brown (*Me.w.b.*), larger, and reach to the middle of the second abdominal segment. They are closely applied to the sides of the body and cover the metathoracic rudimentary buds.

Text-figure 19.



Fourth instar nymph. Male. Lateral view, × 66. Binocc. Ok. 10, Obj. 32 mm. (For explanation of letters, see p. 305.)

The dorsal region of the thorax is humped, and a definite waist appears between the thorax and abdomen; in previous instars the thoracic and abdominal segments were almost the same width.

The abdomen is composed of nine segments, tapering to a point where the external genitalia are developing. I cannot detect an anal orifice.

The last ecdysis takes place in the cocoon, and the woolly secretion adheres to the adult male for some time.

The Fifth Instar Male.

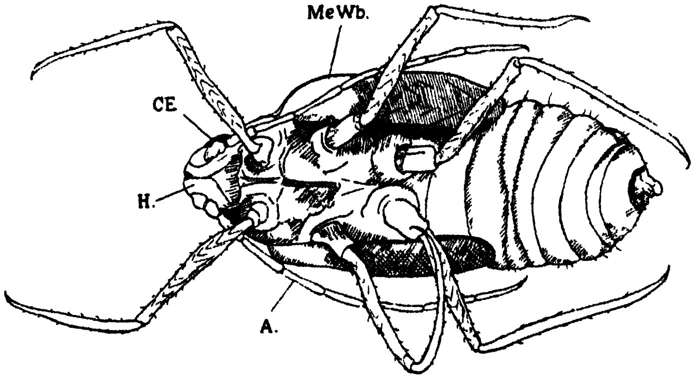
The fifth instar male (text-figs. 21, 22, & 23) is the adult stage, and has the appearance of a small Dipterous fly.

The length of the insect is 2·5 mm. The head (*H.*) is small and the eyes (*CE.*) protrude laterally. The antennæ are very long and slender, being slightly longer than the body of the insect. They are 9-segmented, the proximal two segments being small and the remainder long and thin. They are covered with long setæ. The male waves its antennæ about at right angles to the long axis of its body. The mouth is perfectly obsolete, its place being taken by a chitinous band. Atrophy of the mouth-parts in Coccids frequently takes place during metamorphosis.

The head and thorax together are a little more than half the length of the insect. The thorax is larger than previously, the dorsum and tergum of the mesothorax being humped and strongly chitinised.

The coxæ of the legs are placed in relation to one another as in the fourth instar nymph. The legs are very slender and as long as the body, and bear a single hooked tarsal claw.

Text-figure 20.



Fourth instar nymph. Male. Ventral view, × 66. Binocc. Ok. 10, Obj. 32 mm. (For explanation of letters, see p. 305.)

The upper surface of the last abdominal segment is furnished with a tuft of white bristles, in many cases longer than the insect itself. They are spread out like a fan and elevated during mating.

In the third and fourth instar nymphs there appear to be two pairs of lateral spiracles on the thorax and a lateral abdominal spiracle on each abdominal segment:

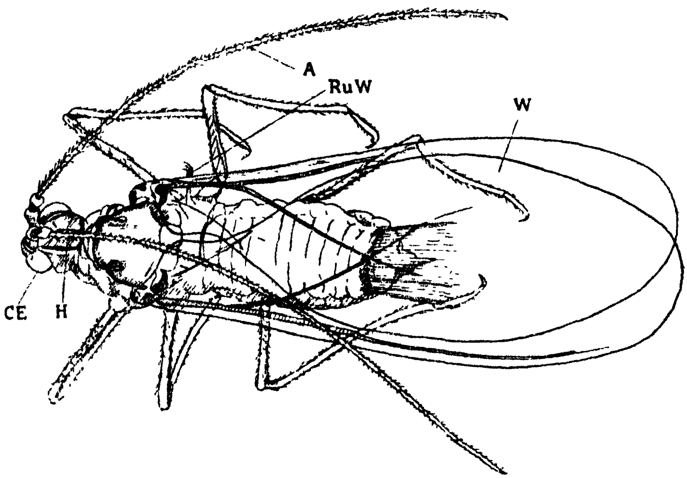
The wings (*W.*) are long and reach beyond the posterior end of the body by more than half the length of the insect. In repose they are crossed over the back of the insect with their surface flat on the dorsal surface of the insect.

The wings are very transparent and rounded at the apex. They have very few veins.

A short spur representing the subcosta (text-fig. 23, *sc.*) lies near the anterior border of the wing. Below this a strong vein runs to the apex of the wing. This is the radius (*R.*). Another vein (*Cu.*) less distinct arises near the base of the radius and runs across the middle of the wing to the anal margin. This may be the cubitus, and the slight thickening above it the medius. There is an indication of an anal vein below this one, but it is very indistinct and uncertain.

The wings of *Orthezia* show other shadowed portions which are not veins, but might easily be mistaken for such. The haltere (text-fig. 23, *RuW.*) has the form of a curved rod, convex on the dorsal border. It is composed of a very stiff chitin, and at its distal end bears three hooked spines (*s.*) on the dorsal aspect which curve to point finally in a ventral direction. The length of the haltere is 220 μ, and the spines at its distal end are 50 μ long. Each lies in repose, in a very small upturned flap in the mesothoracic wing of its side.

Text-figure 21.



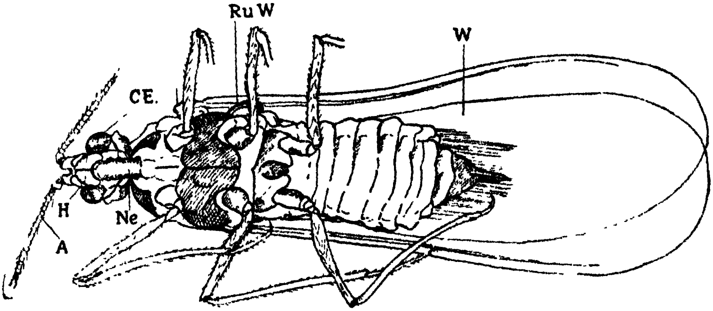
Fifth instar. Adult male. Dorsal view, × 53. Binocc. Ok. 10, Obj. 32 mm.
(For explanation of letters, see p. 305.)

Patch (**29**) and also Comstock (**7**) say that in a wing so highly specialised as that of the Coccid it is not improbable that the tracheation has lost its value as a basis for wing-venation. In her description of the tracheation and venation of the wings of *Dactylopius* and other Coccids, Patch (**29**) says that the tracheæ are in two groups, the dorsal group showing the subcostal and radial tracheæ running close together and crossing and recrossing frequently in their course. Below these two interwoven branches the median tracheæ pursue a common course. Comstock (**7**) says that the median trachea is in the costo-radial group, and perhaps a transverse basal trachea does not divide in Coccidæ.

The second group shows a cubital and an anal trachea running near together.

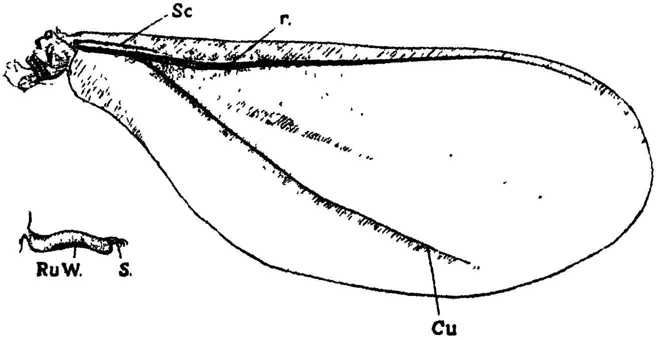
As the tracheæ remained distinct after the veins began to form, it was possible to see, according to Patch (**29**), that one vein, the radius, followed the course of the subcostal and radial tracheæ; another, the medius, followed the course of the first tracheal group, and then followed mainly the median tracheæ across the wing, but in places appeared nearer the course of the cubital trachea.

Text-figure 22.



Fifth instar. Adult male. Ventral view, × 53. Binocr. Ok. 10, Obj. 32 mm. (For explanation of letters, see p. 305.)

Text-figure 23.



Wing. Mesothoracic and rudimentary metathoracic wing. Adult male. Camera. Ok. 2, Obj. Zeiss A. (For explanation of letters, see p. 305.)

Patch (**29**) says that coalescence of tracheæ occurs in Coccids, Psyllids, and Aphids.

Berlese (**3**) and Henneguy (**21**) mention the presence of halteres and their conformity with those of Orthorhaphic Diptera.

Kirchner (**24**) is the only author to describe the male instars of *O. urticæ*, and this is, indeed, a very brief description, owing to lack of material. I cannot detect anything resembling "the two long divergent tail-like appendages of the anal extremity of the first-stage male nymph."

Newstead (**28**) and Imms (**22**) mention that atrophy of the mouth-parts takes place in the pupæ of Coccids

Burmeister (**5**) and Westwood (**32**) describe a male which they attribute to *O. urticæ*, but it seems likely that it is some other species.

LIFE-HISTORY.

The life-history of *O. urticæ* may be briefly described as follows:—The eggs are laid in batches from the end of May until September, and hatch after remaining in the brood-sac for about three weeks, so far as I can ascertain.

In the first and second instars the sexes cannot be distinguished.

The male passes through two larval instars, and then becomes a nymph in which developing wings are visible externally. Two further ecdyses reveal the final or adult instar.

The female passes through three larval instars and then becomes the adult, in which no wings are present.

O. urticæ reproduces parthenogenetically. Young first instar larvæ were obtained in September 1925. These were kept in breeding-cages, and in the spring of 1926 each male, as it became apparent, was removed from the breeding-cage in its nymphal stage. In the summer of 1926 the females of these 1925-hatched Coccids had reached their adult stage and produced young, obviously without the intervention of a male.

Males of this species are extremely rare.

(a) HABITS OF THE LARVÆ. (Pl. I. figs. 1 & 2.)

The eggs are white when laid, but appear pale yellow as the embryo develops. On opening a full brood-sac, the eggs near the genital aperture are seen to be white, while those furthest from it are yellowish to pale brown. The average length of the egg when laid is 0·580 mm. and the width, in the middle, approximately 0·320 mm., the egg being oval. The eggs are laid in a wax pouch formed by the adult female, and are completely surrounded by a pure white woolly secretion, which appears like fine wavy threads, acting as packing for the eggs.

The young larvæ hatch in the brood-sac, and remain there until they have acquired a scant covering of wax secretion, which appears as a slight white pubescence on the dorsal surface. The larvæ crawl out through a split in the wax at the distal end of the maternal brood-sac.

The larvæ are always found feeding on the stem or the veins on the under side of the leaves, preferably on the mid-rib, where there would be the best flow of sap. They insert their piercing stylets far into the juicy vein, so that the distal end of the proboscis rests on the surface of the vein and the proboscis itself (labium) does not enter the tissues. The posterior end of the body is elevated so as to be in a line with the proboscis, and makes an angle of about 30° with the leaf. This position may be retained for hours. When walking, the body is placed parallel to the surface walked on, with the proboscis hanging down at right angles. All movements are sluggish.

The larva secretes a clear, glutinous substance which becomes opaque on exposure to the air. This substance passes out of the anal orifice, and is probably the animal's natural excrement. This is known as the "Honeydew" of Coccids. It is left on the leaves as a black deposit into which a Mycelium penetrates. This, however, apparently does not damage the leaves.

The first instar larvæ (Pl. I. fig. 1) grow rapidly during the summer months, but late broods, hatching at the end of August or beginning of September, remain in the first instar for a longer time, and only have one ecdysis before the winter.

In early summer broods, the second instar lasts for two or three weeks, but August and September broods hibernate in this stage.

During the spring and summer months the larvæ are found on Sage and Stitchwort; but later on, in the autumn, they seem to leave the Stitchwort and are found mainly on the Sage.

The larva moults by first anchoring itself by its proboscis and claws; then a split occurs in the dorsum of the meso- and metathoracic segments and extends into the first two or three abdominal segments. The next instar larva emerges by first pushing out its thoracic segments and then its head. It then crawls forward out of the old skin, which adheres to the hind abdominal segments for some time before falling off.

The white wax armour takes four or five days to complete. An actual example may be given. On May 4th a larva cast its skin, and then appeared pale green with light brown legs and antennæ and no sign of wax. On May 5th it was covered by a slight white pubescence of wax. On May 6th the wax was seen to be arranged in definite divisions. The body was darker. On May 7th plates could be made out protruding sideways, and the anal funnel had begun to form (Pl. I. fig. 1, *al.*) round the anus. The body was covered with wax. On May 10th the plates had increased to their final state.

List (**25**) mentions the preference of the larvæ for the undersides of leaves. Newstead (**28**) and Amyot and Serville (**1**) mention the honeydew of Coccids. Newstead (**28**) says that the sexes are rarely distinguishable in larval Coccids; I am inclined to think that the second instar males are longer in proportion to their width than the females. Schmidt (**30**) says that in the Coccid *Aspidiotus nerii* the sexes are indistinguishable in the young larvæ, but he thinks the later male larvæ are more slender than the female.

(b) HABITS OF THE FEMALE. (Pl. I. fig. 3, Pl. II. fig. 4.)

After the second instar the sex of any individual is distinguishable. The third instar female and the adult move sluggishly about on the food-plant as do the larvæ. The general activities, mode of feeding, and method of ecdysis of the third and fourth instar females are similar to those of the larvæ. The third instar female stage lasts only a week under favourable conditions, but late autumn females of this instar remain in this stage to hibernate through the winter, not moulting until the following April or May.

At the end of April or beginning of May the adult female insect shows signs of developing the brood-sac (Pl. II. fig. 4, *Bp.*). The eggs are laid in the brood-sac, which entirely obscures the genital aperture, which is situated on the ventral side of the last abdominal segment.

The young larvæ hatch in the brood-sac and remain there for about two days before emerging.

The adult females always crawl to a quiet corner of the breeding-cage, or under dead leaves, during the time of egg-laying, where they remain without feeding, often for more than a week. When the larvæ are about to emerge from the brood-sac, the mother crawls up a fresh twig of sage and clings to the stem in a perpendicular position, while the larvæ emerge downwards and creep away on to the veins on the ventral side of the leaves. It is a common sight among colonies of *Orthezia* to see the old female on the underside of a leaf surrounded by so many young that they make the veins appear as though painted thickly with white paint.

During the course of the four instars the female grows wider in proportion to her length, so that the adult female appears circular in dorsal view.

The female remains in its four instars for a variable length of time according to the time of the year, the shortest life-cycle, in hot dry weather, taking about six to seven weeks to complete.

The larvæ and later female instars seem to be able to endure cold and wet to a fairly large extent, but prefer a dry aspect and become more active in the warmth and sun.

An adult female produces a variable number of young. From several females, which I observed closely, I obtained an average of 60 per female. These did not all emerge at one time, but frequently 18–20 emerged in each of three distinct broods with intervals of about a week between each hatch.

Among the young larvæ and eggs in the brood-sac of the female I found a number of parasitic mites crawling about in the woolly secretion surrounding the growing young. Probably I obtained fewer young from my captive adults than I should have done had the brood-sac been free from parasites. Edwards (18), in a brief outline of the life-history of *Orthezia*, calls the entire state intervening between egg and adult by the term nymph. Kuhni Kannan (23) records four female instars of

O. insignis, and says that the interval between successive moults is about two weeks.

Several captive adult females, after producing broods in summer, 1926, lived through the ensuing winter and began to feed again in February, but in July had not shown any further signs of reproducing. This disagrees with Newstead's (**28**) statement that female Coccids never winter in the adult stage. Probably they cannot live through the winter in their natural exposed state.

Amyot and Serville (**1**) say that l'Abbé d'Orthez (**9**) found 85 young and 15 eggs in one brood-sac. Kuhni Kannan (**23**) gives 80–110 as the numbers of a complete brood in *O. insignis*, and Kirchner (**24**) records 80 for *O. urticæ*. These are all larger broods than I obtained, which is probaby due to the influence of the parasitic mite.

Kirchner (**24**) and Amyot and Serville (**1**) found a beetle larva, *Hyperaspis repensis*, parasitic in the brood-sac, and the latter authors mention that it devours the young as they hatch.

(c) HABITS OF THE MALE. (Text-figs. 17–22.)

The Third Instar Male.

At the end of February and beginning of May during the second instar, the male larva crawls to a corner or selects a curled dry leaf or the angle between the leaf and stem of a twig. In the breeding-cage the favourite place was the top corners of the woodwork. The larva remains here quiescent for at least a fortnight. It then moults, and the third instar (text-figs. 17 & 18) takes the form of a nymph possessing a pair of mesothoracic wing-stumps showing externally. The nymph secretes, from dermal glands, a flocculent enveloping cocoon, which is white, tinged with pale green, and extends from the insect to a distance of about half an inch. The nymph lies quiescent, but if disturbed, first walks slowly away, and then stiffens and shams death, with its legs bent up. The secreting of the cocoon takes about two days to complete.

The Fourth Instar Male.

After four days to a week the nymph again moults and assumes the second nymphal stage, which is the fourth instar (text-figs. 19 & 20). The wing-buds (*Me.w.b.*) are longer, and the nymph has assumed the general body appearance and shape of the adult male. On ecdysis the nymphal skin splits along the back and the nymph emerges backwards, in contrast to the larva, which emerges forwards. The nymph crawls out of its third instar nymphal cocoon, leaving the exuvium behind, and the fourth instar nymph immediately begins to secrete a new cocoon of exactly the same type as the last, close to or at some little distance away from it. This second nymph is quiescent, but moves away if disturbed. It remains in this stage for a week or nine days; then ecdysis takes place once more, and the adult winged male emerges as the fifth instar (text-figs. 21 & 22).

The Fifth Instar Male.

There are exceedingly few males developed compared with the number of females. During the spring of 1926 I only obtained about twelve.

The mouth of the male is sealed, there being no feeding during the final instar.

The adult male crawls about on the leaves and twigs and rarely flies, and then only for short distances from leaf to leaf. It crawls about among the larvæ and females, and selects either a third instar larval or an adult female, and copulation follows. This is intermittent and lasts for about an hour and a half. The male then dies, about five hours after copulation. This fact, that males mated with undeveloped females, I have observed in several cases.

I have, on several occasions, watched a newly-emerged male put among adult and larval females, and in no case did the male mate with more than one particular female, and, although it frequently wandered away from her, it always sought her out again, passing by any others it met on the way. Continuous observations of the movements of the male for 2–3 hours during copulation were made, the actions which took place during that time being noted. In one case, where the final moult began in the early morning and was complete by 11 A.M., the male began to walk away from the cocoon at 2 P.M., and the wings were then stretched. It returned to the nymphal cocoon in the evening, and did not seek a mate until two days later, remaining quiescent for all the intervening day. At 9.30 A.M. on the third day of its adult existence, the male chose a third instar female, copulation followed, accompanied by excited movements of the legs, antennæ, and wings. The position assumed by the male, mounted on the back of the female, was almost always identical. The prothoracic legs rested on the median wax plates of the dorsal region of the female abdomen, the mesothoracic legs gripped the posterior aspect of the female abdominal plates, and the metathoracic legs of the male gripped the fourth and fifth abdominal sterna. The legs moved continually up and down as though marking time. The anterior pair of legs of the male were pressed close together on the median line of the dorsal abdominal places. They then moved about 1 mm. apart, and then touched together again at intervals in an excited manner. The wings were raised and spread slightly apart at an angle of about 45° with the body. The white tufts at the end of the male abdomen were raised and stretched out parallel to the wings.

During mating the female assumed the inclined feeding position, with her body raised posteriorly at an angle of about 45° with the substratum. She moved forward slowly at the rate of about half an inch in seven and a half minutes.

The adult males which I obtained in captivity never lived more than 48–72 hours.

The fecundated undeveloped females (third instar), which I separated under glass cylinders, unfortunately died without further moult, though in some cases living through the winter or for some six or eight months, so that I have not yet further investigated this peculiar occurrence of fertilisation of undeveloped females.

The males attain their adult stage earlier than the females, being found in small numbers for nearly three and a half months from the beginning of March in a warm spring until the middle of June. I found no more males during the year after June.

Douglas (**11**), on *Orthezia*, refers to fertilisation of undeveloped females, and Amyot and Serville (**1**) say "the females are subject to moulting after pairing, but not so frequently as before."

According to Newstead (**28**) there are only three instars in the male of *O. insignis*. He never found a male *O. urticæ*. He says that after one moult the nymphal instar is obtained with external wing-pads. It seems unlikely that a species so nearly allied to *O. urticæ* should have two less instars in its life-history. Schmidt's (**30**) five instars for *Aspidiotus nerii* agree with my findings in *Orthezia*. Imms (**22**) says that three female and four male instars are the most common among Coccids.

Kirchner (**24**) records males from the second half of May and no earlier. Amyot and Serville (**1**) found males in September "after three or four moults."

SUMMARY.

All stages of the Coccid Bug, *O. urticæ*, were collected and bred in the laboratory to investigate the number of instars and the morphology.

The first and second instar larvæ are sexually indistinguishable. The male has two larval, two nymphal, and a winged adult stage. The female has three larval and a wingless adult stage.

Breeding and growth take place rapidly between May and the end of August. The males attain the adult stage in March, and are found in very small numbers until the middle of June. The females begin to form their brood-sacs in May or June, and reproduce throughout the summer months. From the beginning of September to the end of January the insects hibernate.

The occurrence of *O. urticæ* in its different instars is summed up in the table see (p. 303), from the events noted during the time I have had the Coccids under observation.

In the external morphology it is noticeable that there is a breaking-up in the wax plates to coincide with the segmentation of the insect, and extra intermediate blocks are cut off from the originally-placed main blocks. The glandular setæ become more numerous from the first to fourth instar of the female, and the outline of the insect becomes almost circular, the abdomen shortening considerably in the adult stage. The male nymph of the third and fourth instars possesses external wing-stumps on the mesothorax, and an indication of metathoracic halteres is seen on the fourth instar nymph. The adult male has a pair of mesothoracic wings, but flies very little and only lives for a few days.

Table of Life-history of O. urticæ.

INSTAR.	FEMALE.	MALE.
1	Larva.	Larva.
2	Larva.	Larva.
3	Larva.	Nymph (external wing-pads).
4	Apterous adult.	Nymph (external wing-pads).
5	—	Alate adult.

Table to show which instars may be found in each month of the year, both out of doors and in captivity. September 1925 *to August* 1926.

MONTH.	WOOD END.	LABORATORY.		
1925.				
September	1, 2, 3, 4 (instars).	1, 2, 3, 4, put in cage.		Female instars.
	1, 2.	1, 2.		Male „
October	1, 2, 3, 4.	1, 2, 3, 4.		Female „
	1, 2.	1, 2.		Male „
		*(*a*).	(*b*).	
November	2, 3.	2, 3,	2, 3.	Female „
	2.	2,	2.	Male „
December	2, 3, hibernating.	2, 3, hibernating.	2, 3.	Female „
	2, „	2, „	2.	Male „
1926.				
January	2, 3, „	2, 3, „	2, 3.	Female „
	2, „	2, „	2.	Male „
February	2, 3, slight activity.	All died except six.	2, 3.	Female „
	2, „ „		2, 3, 4, 5.	Male „
		*(*a*) = Kept in moss etc. in cold. (*b*) = Kept in warmth.		
March	2, 3, slight activity.	2, 3.		Female „
	2, „ „	2, 3, 4, 5.		Male „
April	2, 3, active.	2, 3.		Female „
	2, 3, 4, 5, active. (3, 4, 5, only at end of month).	2, 3, 4, 5.		Male „
May	2, 3, 4.	2, 3, 4.		Female „
	2, 3, 4, 5.	2, 3, 4, 5.		Male „
June	1, 2, 3, 4 } 1st only at end of month.	1, 2, 3, 4 } 1st only at end of month.		Female „
	1, 2, 3, 4	1, 2, 3, 4		Male „
July	1, 2, 3, 4.	1, 2, 3, 4.		Female „
	1, 2.	1, 2.		Male „
August	1, 2, 3, 4.	1, 2, 3, 4.		Female „
	1, 2.	1, 2.		Male „

LITERATURE REFERENCES.

1. Amyot et Serville. (1843.) ‘Hémiptères.’
2. Balfour-Browne, F. (1909.) “The Life-history of the Agrionid Dragonfly.’ Proc. Zool. Soc. 1909, p. 253.
3. Berlese, A. (1909.) ‘Gli Insetti.’
4. Bosc *. (1784.) “*Orthezia characias.*” Journal de Phys. tom. xxiv.
5. Burmeister *. (1835.) ‘*Dorthezia urticæ.*’ Hanb. ii.
6. Carpenter, J. H. (1913.) ‘Life-history of Insects.’
7. Comstock, J. H. (1918.) ‘The Wings of Insects.’
8. De Geer *. (1778.) ‘*Coccus floccosus.*’ Mem. vii.
9. D'Orthez *. (1785) “Observations sur le Coccus, *Dorthesia characias.*” Journal de Phys. xxvi.
10. Douglas, J. W. (1880-81.) “On the Species of the Genus *Orthezia.*” Ent Mo. Mag. xvii.
11. —— (1881.) “Observations on the Species of the Homopterous Genus *Orthezia*, with a Description of a New Species.” Trans. Ent. Soc.
12. Dufour, L. (1833.) “Recherches Anatomique et Physiologiques sur les Hémiptères.” Mém. Sav. etr. Acad. Sci. Paris, iv.
13. Edwards, J. (1896.) ‘The Hemiptera-Homoptera of the British Isles.’ London.
14. Fabre, J. H. (1923.) ‘The Life of a Scorpion.’
15. Fabricius *. (1794.) “*Coccus dubius.*” E. S. iv.
16. Ferris. (1918.) “A Note on the Occurrence of Abdominal Spiracles in the Coccidæ.” Can. Ent.
17. Frisch *. (1730.) “Von der wiessen Blatt Lause auf der matricaria.” Beschr. v. Allerly Insecter von Teutschland, viii.
18. Fürth, O. von. (1903.) ‘Vergleichende de chemische Physiologie den niederen Tiere.’
19. Green, E. E. (1917–19.) “List of Coccidæ affecting various Plants.” Ann. of App. Biol. 4, 5.
20. —— (1921.) “Observations on British Coccidæ, with Descriptions of New Species.” Ent. Mo. Mag. Lond. no. 79, 3rd ser.
21. Henneguy, H. L. (1904.) ‘Les Insectes.’
22. Imms, A. D. (1925.) ‘Text-book of Entomology.’
23. Kuhni Kannan, K. (1920.) “Life-history of *O. insignis.*” Report Proc. 3rd Ent. Meeting, Pusa, Feb. 1919, Calcutta, iii.
24. Kirchner, R. (1912.) “Zur Entwicklungsgeschichte und Lebenweise von *O. urticæ.*” Stuttgart Jahreschefte ver Natk. lxviii.
25. List, J. H. (1887.) “*Orthezia cataphracta* eine Monographie.” Zeitschrift. für Wissenschaftliche. Zoologie Kolliker, xlv.
26. Linné *. (1767.) “*Aphis urticæ.*” S. N. 736.
27. Mammen, H. (1912.) “Ueber die Morphologie der Heteropteren und Homopterentstigmen.” Zool. Jahrb. Abth. Morph., Bd. xxxiv.
28. Newstead, R. (1902.) ‘A Monograph of the British Coccidæ.’ Vol. ii. Ray. Soc.
29. Patch, E. M. (1909.) “Homologies of the Wing-veins of the Aphidæ, Psyllidæ, Aleurodidæ, and Coccidæ.” Ann. Ent. Soc. Am. ii.
30. Schmidt, O. (1885.) “Metamorphose und Anatomie des männlichen *Aspidiotus nerii.*” Archiv für Naturges 1, L. i.
31. Signoret *. (.) “Essai sur les Cochinelles ou Gallinsectes.” Ann. Soc. Entom. de France, 5th ser., tom. v.
32. Westwood, J. O. (1840.) ‘Insects.’ Vols. i. & ii.
33. Wintersterin, H. (1911.) ‘Handbuch der vergleichenden Physiologie.’ 2 Band. Stoffwechselt. Sweite Hälfe.
34. Zetterstedt *. (1840.) “*Dorthesia urticæ.*” Ins. Lap. 314.

* References not obtained, but referred to by Douglas or List.

Lettering of Figures.

A. Antennæ.
A. 1–8. Segments of antennæ.
Ant. Anterior.
ab. 4–10. Abdominal segments.
abp. Abdominal pyramids.
absp. Abdominal spiracles.
al. Anal wax tube.
ao. Anal orifice.
ap. Anal plate.
Bp. Brood-sac.
Br. Anal bristles.
C. Coxa.
CE. Compound eye.
Cu. Cubitus.
c.f. Chitinous folds.
Ch. Cephalic wax plates.
Ch.p. Chitinous anal plate.
d.p. Dermal pores.
E. Simple eye.
ec. Extra cone of eye.
F. Femur.
g.s. Glandular setæ.
gu. Gustatory organs.
H. Head.
h. Hypodermis.
im.b. Imaginal wing-bud.
ip. Intermediate plates.
le. Lens.
Me.w.b. Mesothoracic wing-bud.
Mp. Marginal plates.
me.d.p. Mesothoracic dorsal plate.
Mt.d.p. Metathoracic dorsal plate.
Ne. Neck.
P. Proboscis.
pd. Depression on femur.
pdp. Prothoracic dorsal plate.
pt. Pear-shaped tube.
R. Radius.
RuW. Rudimentary wing.
RuWb. Rudimentary wing-bud.
S. Setæ.
s. Spines.
sb. Spiracular bulb.
sc. Subcosta.
spc. Spiracular cone.
sp.t. Spiracular tube.
Sy. Stylets.
T. Tibia.
Ta. Tarsus.
Tc. Tarsal claw.
Th. 1–3. Thoracic wax plates.
Ts. Terminal spine.
T.sp. Thoracic spiracles.
W. Wings.
x. Special setæ.

EXPLANATION OF THE PLATES.

Plate I.

Fig. 1. First instar larva with wax secretion. Dorsal view, × 175. Binocc. Oc. 10, Obj. 48 mm.
Fig. 2. Second instar larva with wax secretion. Dorsal view, × 100. Binocc. Oc. 10, Obj. 48 mm.
Fig. 3. Fourth instar larva with wax secretion. Dorsal view, × 45. Female. Binocc. Oc. 10, Obj. 48 mm.

Plate II.

Fig. 4. Fourth instar. Adult female with brood-sac and wax secretion. Dorsal view, × 28. Binocc. Oc. 10, Obj. 48 mm.
Fig. 5. Second instar larva. Male. With wax secretion. Ventral view, × 110. Binocc. Oc. 10, Obj. 48 mm.

15. On Abnormalities in *Rana temporaria* chiefly affecting the Vascular System.

By J. H. Lloyd, M.Sc. (Birm.), F.Z.S., Lecturer in Zoology and Comparative Anatomy, University College, Cardiff.

[Received March 7, 1928: Read April 17, 1928.]

(Text-figures 1–7.)

Most of the specimens described in these notes were observed during the dissection of many hundreds of frogs for class purposes in the course of the last few sessions. All the frogs belonged to the species *Rana temporaria.*

Specimen A.

This animal possessed two distinct normal-sized spleens attached to the mesentery in the usual position dorsal to the stomach. The animal was perfectly normal in all other respects. Sex not noted.

Specimen B. (Text-figure 1.)

This specimen was a male. In it the anterior abdominal vein, instead of opening in the normal manner into the liver and hepatic portal vein, opened into the left subclavian vein, just before the latter united with the internal and external jugular veins to form the left anterior vena cava. The abdominal vein was abnormally large.

The sole supply of venous blood to the liver was through the hepatic portal vein, and the posterior vena cava was normal.

It is interesting to compare the condition seen in this specimen with that found in *Ceratodus* (**5** and **15**), where the anterior abdominal vein opens into the right ductus Cuvieri and a persistent posterior cardinal vein opens into the left ductus Cuvieri.

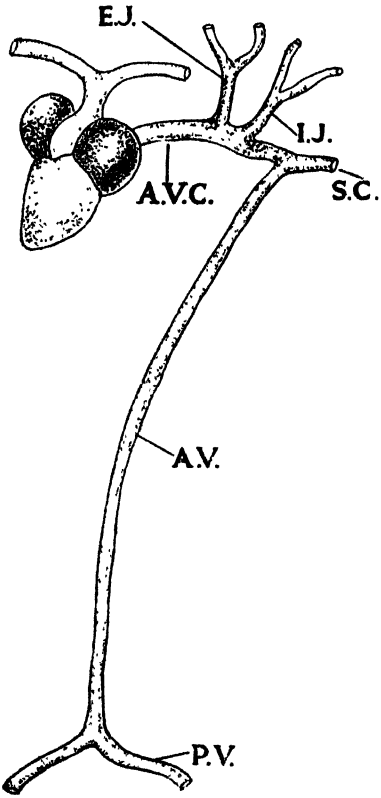
During embryonic development the anterior abdominal vein of the frog originates by the fusion of a pair of larval veins which convey blood from the hind limbs to the sinus venosus. Later the connection to the sinus venosus is normally lost, so that its persistence in this specimen represents, as has been pointed out by previous writers, a persistent embryonic condition.

The condition observed in this specimen has been previously noted, with variations in detail, by Buller, 1896 (**1**); Woodland, 1910 (**18**); O'Donoghue, 1911 (**11**); Collinge, 1915 (**2**); and lastly by Eales, 1925 (**3**).

Specimen C. (Text-figure 2.)

This was a female which showed a primitive condition of the renal portal veins. According to Hochstetter (6), the posterior cardinal veins, in the region of the kidney (mesonephros), form two main channels, an inner and an outer. The inner channel eventually fuses with its fellow to form the inter-renal portion of the posterior vena cava. The outer channel loses its connection with the posterior cardinal vein anteriorly and becomes eventually the renal portal vein. In the specimen now described both right and left renal portal veins are continued forwards around the anterior borders of the kidneys and unite with the posterior vena cava. There is, however, no connection posteriorly

Text-figure 1.

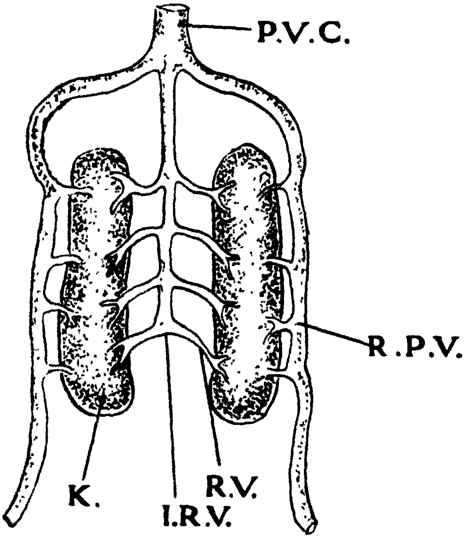


A.V. Anterior abdominal vein. A.V.C. Anterior vena cava. E.J. External jugular vein. I.J. Internal jugular vein. P.V. Pelvic vein. S.C. Subclavian vein.

between the renal portal veins and the inter-renal portion of the posterior vena cava.

A condition similar to that seen in this specimen has been described by Shore, 1900 (**14**) and Collinge, 1915 (**2**). In their examples, however, the abnormality occurred on the left side of the body only. Both these writers suggest that the most probable explanation of this abnormal vein "is that it is a persistent part of the left posterior cardinal vein which normally disappears during the later parts of larval life." This explanation would hold good in the present case, except that here portions of both right and left posterior cardinals have persisted.

Text-figure 2.



I.R.V. Inter-renal vein. K. Kidney. P.V.C. Posterior vena cava. R.P.V. Renal portal veins. R.V. Renal veins.

Specimen D. (Text-figure 3.)

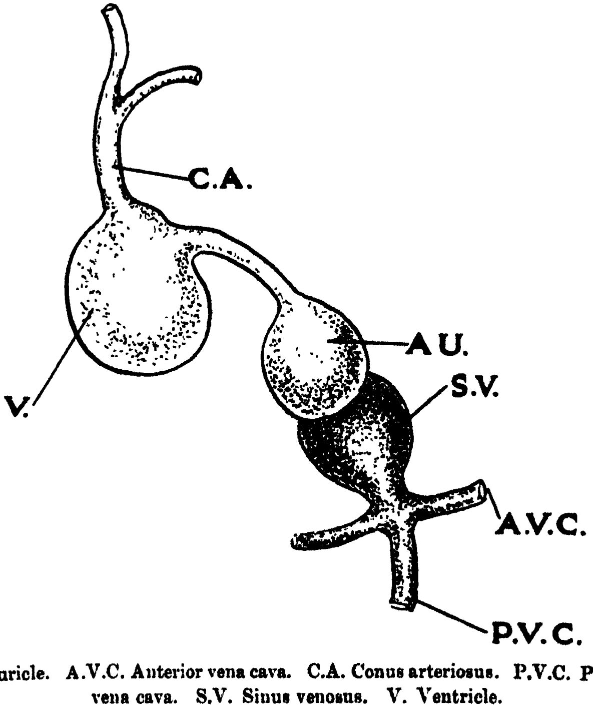
This specimen, which was a male, was given to me some years ago by the late Professor W. N. Parker in a bottle which was labelled "Frog with two hearts?" The examination of the specimen, however, has shown that, although at first sight there appeared to be two hearts present, in fact there was only one. This heart was, however, of a primitive type closely comparable to that of an Elasmobranch fish.

A thin-walled sinus venosus, which received both right and left anterior venæ cavæ and the posterior vena cava, lay dorsal to and opened into a single thick-walled auricle. The auricle lay close to the left side of a large thick-walled ventricle, to which it was joined by a narrow tubular stalk. A conus arteriosus was given off normally from the ventricle, and divided into the three main arterial trunks on each side.

As the specimen had been in spirit for several years, it was not possible to trace the pulmonary veins, and injection was, of course, impossible in a specimen which had lost all its elasticity.

The only other case of a somewhat similar heart, which I have been able to trace as recorded, was described by Lyle, 1899 (9), but his specimen differed from that described here in several important features.

Text-figure 3.



AU. Auricle. A.V.C. Anterior vena cava. C.A. Conus arteriosus. P.V.C. Posterior vena cava. S.V. Sinus venosus. V. Ventricle.

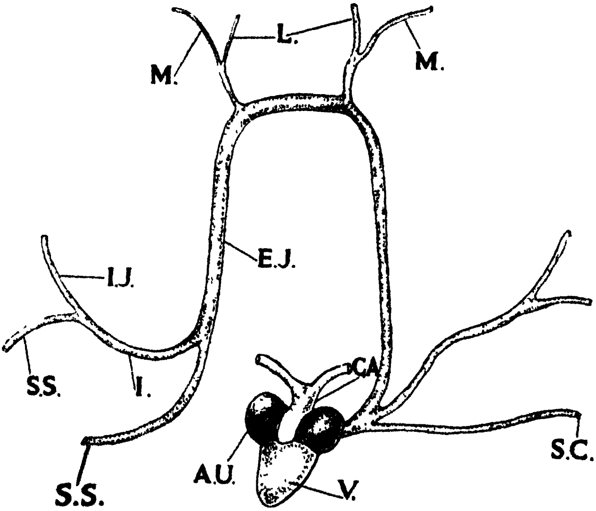
In Lyle's specimen the chambers were arranged more or less in line, the sinus venosus, which was the most posterior, being followed by an "accessory chamber" (to the auricle), an auricle with an incomplete septum, a ventricle, and a conus arteriosus. The posterior vena cava opened into the sinus venosus, as did also the pulmonary veins, but the right and left anterior venæ cavæ opened into the auricle.

Specimen E. (Text-figure 4.)

This specimen was a male which was characterised by the complete absence of a right anterior vena cava. The veins which normally unite to form the right vena cava were joined to the left external jugular by an anterior connecting branch, which arose from the anterior end of the right external jugular vein. The right external jugular vein was abnormally large, but the right mandibular and lingual veins were smaller than the corresponding veins on the left side.

The right subclavian and innominate veins were normal. All the blood from the right side ultimately passed into the left anterior vena cava.

Text-figure 4.



AU. Auricles. C.A. Conus arteriosus. E.J. External jugular. I. Innominate vein. I.J. Internal jugular. L. Lingual. M. Mandibular vein. S.C. Subclavian vein. S.S. Subscapular vein. V. Ventricle.

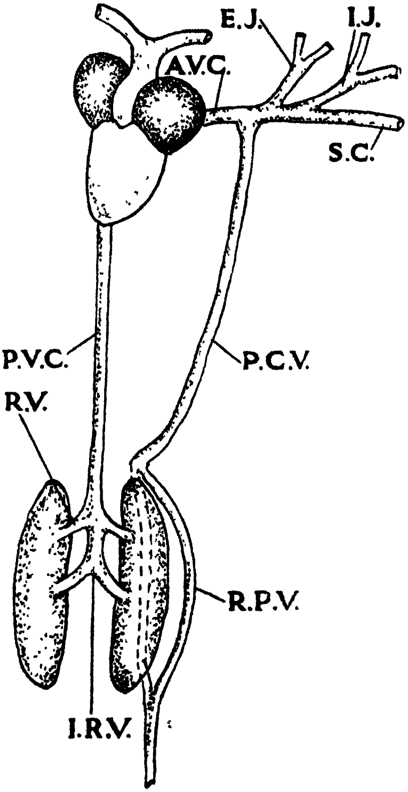
Flattely, 1926 (**4**), mentions an example which appears to differ, from the one described here, in the fact that the connection between the jugulars was situated more posteriorly.

White-Thompson, 1927 (**16**), has recently described a specimen which agrees very closely with my specimen E.

Specimen F. (Text-figure 5.)

This specimen was a female, and was characterised by the presence of the left posterior cardinal vein, which opened anteriorly into the anterior vena cava. Posteriorly the persistent cardinal was continuous with the renal portal vein. In addition, a branch was given off by the renal portal vein, which ran dorsal to the kidney and joined the posterior end of the persistent cardinal near the anterior border of the kidney.

Text-figure 5.



A.V.C. Anterior vena cava. E.J. External jugular vein. I.J. Internal jugular vein. I.R.V. Inter-renal vein. P.C.V. Posterior cardinal vein. P.V.C. Posterior vena cava. R.P.V. Renal portal vein. R.V. Renal vein. S.C. Subclavian vein.

The posterior vena cava was normal, except for the fact that the inter-renal portion was short and only received two renal veins on each side.

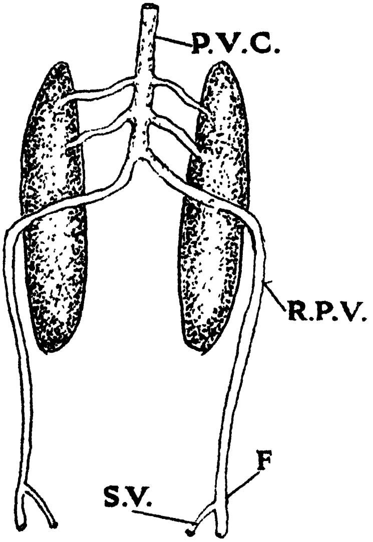
Persistent cardinal veins have previously been noted by Howes, 1888 (7); Parker, 1889 (13); Woodland, 1905 (17); O'Donoghue, 1910, 1913 (10 and 11); Collinge, 1915 (2); and Lloyd, 1921 (8).

Specimen G. (Text-figure 6.)

This specimen was a male. The femoral, sciatic, and pelvic veins were normal, and the two former on each side united in the usual manner to form the renal portal veins. These, however, after running along the outer borders of the kidneys for about half their length, turned and ran across the ventral surfaces of the kidneys to unite with the posterior vena cava.

The only other case which I have been able to trace that resembles this at all was described by Collinge (2). In his specimen the condition on the right side was similar to that described above, but the left renal portal vein was entirely absent.

Text-figure 6.



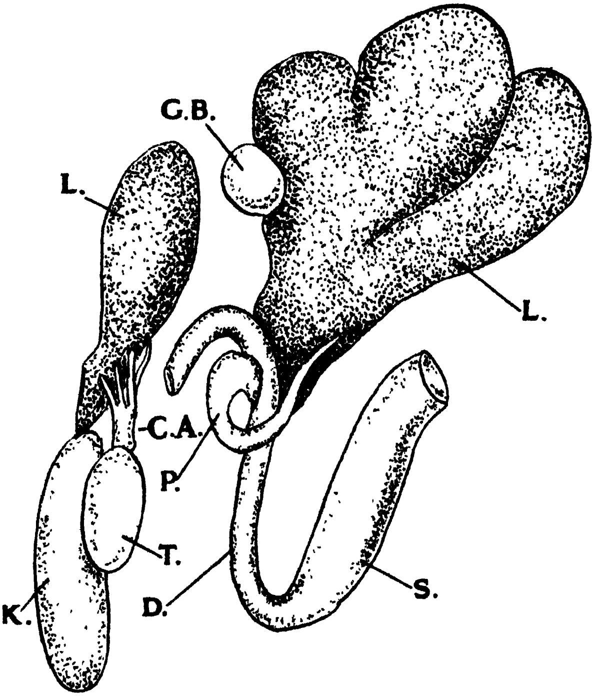
F. Femoral vein. P.V.C. Posterior vena cava. R.P.V. Renal portal vein. S.V. Sciatic vein.

Specimen H. (Text-figure 7.)

This animal was a male. The pancreas was absent from the normal position between the stomach and duodenum. A small lobe, however, was present, attached to the distal end of the duodenum, from which a band looped around the duodenum and joined the outer lobe of the left lobe of the liver. This bridge of tissue was apparently composed of liver and pancreas, the pancreatic portion being mesial.

The right lobe of the liver was reduced to about a quarter of its normal size, and was fused to the anterior end of the right corpora adiposa. This latter structure was also attached normally to the testis. The posterior end of the right lobe of the liver was attached to the outer border of the right kidney. I was unable to trace any bile-ducts from the right lobe of the liver.

Text-figure 7.



D. Duodenum. C.A. Corpora adiposa. G.B. Gall-bladder. K. Kidney. L. Liver. P. Pancreas. S. Stomach. T. Testes.

References to Literature.

1. Buller, A. H. R. Abnormal Anterior Abdominal Vein in a Frog. Journ. Anat. & Physiol. xxx. 1896, p. 211.

2. Collinge, W. E. Some Abnormal Developments in the Vascular System of the Frog. Journ. Anat. & Physiol. vol. l. 1915, p. 87.

3. Eales, N. B. Three Cases of Abnormal Anterior Abdominal Veins in the Frog. 'Nature,' London, cxv. no. 2895, 1925, p. 606.

4. Flattely, F. W. Abnormal Venous Circulation in a Frog. 'Nature,' London, cxviii. no. 2958, 1926, p. 50.

5. Goodrich, E. Treatise on Zoology. Ed. Ray Lankester. Part ix. Vertebrata craniata.

6. Hochstetter, F. Beiträge zur vergl. Entwicklungsgeschichte des Venensystems der Amphibien und Fische. Morphol. Jahrb. Bd. 13, 1888.

7. Howes, G. B. Note on the Azygos Vein in the Anurous Amphibia. Proc. Zool. Soc. 1888, p. 122.

8. Lloyd, J. H. Abnormalities in the Common Frog (*Rana temporaria*). Proc. Zool. Soc. 1921, p. 493.

9. Lyle, H. W. Abnormal Conditions of Circulatory System of the Frog. Proc. Physiol. Soc. in Journal of Physiology, vol. xxiv. 1899, p. vi.

10. O'Donoghue, C. H. The Persistence of Posterior Cardinal Veins in the Frog, together with some Remarks on the Significance of the Renal Portal System. Anat. Anz. Bd. 36, 1910.

11. —— Zool. Anz. Bd. 37, 1911.

12. —— Further Instance of the Persistence of Posterior Cardinal Veins in the Frog. Anat. Anz. Bd. 43, 1913.

13. Parker, W. N. On the Occasional Persistence of the Left Posterior Cardinal Vein in the Frog, with Remarks on the Homologies of the Veins in the Dipnoi. Proc. Zool. Soc. 1889, p. 145.

14. Shore, T. W. Unusual Arrangement of the Renal Portal Vein in the Frog. Journ. Anat. & Physiol. 1900, vol. xxxiv. p. 34.

15. Spencer, W. B. *Ceratodus*. The Blood-Vessels. Macleay Memorial Volume, 1892.

16. White-Thomson, C. R. An Abnormal Specimen of *Rana temporaria*. Ann. & Mag. Nat. Hist. ser. 9, vol. xx. no. 120, 1927, p. 609.

17. Woodland, W. On a New Mode of Persistence of the Posterior Cardinal Vein in the Frog; with a Suggestion as to the Phylogenetic Origin of the Post-Caval Vein. Zool. Anz. Bd. 28, 1905.

18. Woodland, W. Zool. Anz. Bd. 35, 1910.

16. Some Copepoda from Tanganyika collected by Mr. S. R. B. Pask. By Robert Gurney, D.Sc., F.Z.S.

[Received February 22, 1928 : Read April 3, 1928.]

(Text-figures 1–8.)

The following notes on Copepoda are the result of working out some collections made by Mr. Pask in 1926. Some of these collections are plankton taken in open water from a boat, while others were taken by towing a net in the shallow water by the shore when wading. All, however, seem to contain littoral species more than those of the plankton, and the tubes contain a mass of detritus, among which the relatively few Copepods have to be diligently sought for. As all the species are very small, it is quite possible that some species may have been overlooked. A characteristic of the samples is the large number of empty skins of *Schizopera* and young *Cyclops*. The abundance of the fish-parasite *Ergasiloides* is also noteworthy.

It is to be regretted that Mr. Pask was not allowed greater opportunity to collect the Entomostracan fauna, since it is evidently as peculiar as the fishes and other groups of which so much is already known.

The Entomostracan fauna of Tanganyika is as remarkable for the absence of forms which might be expected to occur as for the presence of numerous endemic species. The entire absence of Cladocera from the lake has been noted by Cunnington as one of its most remarkable features. This absence is the more striking in that Cladocera do occur in waters directly connected with the lake. Thus Cunnington (1920, p. 568) says that he found various species in tow-nettings taken in the mouth of the Lofu River, which enters the lake at its south-western corner. Mr. Pask's collection includes a sample (No. 413 F) which was taken among weeds in the blocked-up river-mouth at Kirando (east shore near south end), and this sample contains the following species:—

Cladocera.

Pseudosida szalayi Daday.
Macrothrix triserialis Brady
(syn. *M. chevreuxi* G. & R.).
Chydorus sp.

Copepoda.

Cyclops (s. lat.) *leuckarti* Cls.
„ *varicans* Sars.
„ *agiloides* Sars.
„ *prasinus* Fisch.

Not one of these species occurred in the samples taken from the lake itself *, and all, with the exception of *Pseudosida* and to some extent *C. agiloides*, are species of enormously wide distribution.

---

* *C. varicans* and *C. leuckarti* are recorded from the lake by Sars.

Cunnington suggests (1920, p. 570) that the absence of Cladocera is due to excess of magnesium salts in the water, and there is reason to believe that these salts are toxic to some Cladocera (*Daphnia*). That there is some toxic influence at work is shown also by the facts relating to the Rotifera and Algæ (Cunnington, 1920, p. 569).

The Entomostracan fauna is noteworthy also for the absence of any species of *Canthocamptus* or of any species of the restricted genus *Cyclops*, while only one species of *Diaptomus* is present as against two in Lake Victoria. On the other hand, we find a remarkable wealth of closely-allied forms of the genera *Eucyclops* and *Microcyclops*, which seems to indicate a kind of explosive evolution from a few primary inhabitants. It appears that the waters of Lake Tanganyika are not easily colonised by Entomostraca, but that those species which effect a footing are apt to break up into groups of numerous distinct species.

CALANOIDA.

DIAPTOMUS SIMPLEX Sars.

This is the only species hitherto found in Tanganyika, and I have seen but few specimens in Mr. Pask's collection.

CYCLOPOIDA.

CYCLOPIDÆ.

CYCLOPS O. F. M.

Prof. Sars's subdivision of the old genus *Cyclops* (1918), while excellent in itself, was unfortunately made without regard to previous work, with the result that some of his generic names must lapse in favour of those of Claus. Kiefer (1927) has attempted a revised grouping of the Cyclopidæ, has restored some of Claus's names, and has introduced a number of new ones; but it is doubtful if his conclusions will be accepted generally. On one point in nomenclature he seems to be at fault. *Paracyclops* Claus (1893) was founded for *C. phaleratus* and *C. fimbriatus*; consequently the former should be the type. If, then, the two species are to be separated, it is *fimbriatus* and not *phaleratus* that should be removed to a new genus—in this case to *Platycyclops* Sars. *Ectocyclops* Brady will then remain a synonym of *Paracyclops* instead of replacing *Platycyclops* with *phaleratus* as its type. On general grounds, too, it seems most undesirable to supersede a genus such as *Platycyclops* Sars by a genus so ill-founded as Brady's *Ectocyclops*. The question of the relationship of the three forms *C. phaleratus*, *C. fimbriatus*, and *C. affinis* is by no means clear; probably each should be the type of a genus—*Paracyclops* Claus, *Platycyclops* Sars, and *Heterocyclops* Claus. One of the species described below is evidently most closely related to *C. phaleratus*, and I refer it to *Paracyclops* Claus (but not *Paracyclops* Kiefer), while I include *C. oligarthrus* Sars in *Platycyclops* Sars. The relationships of the many species with the rami of the legs two-jointed and the fifth legs reduced and one-jointed is still in doubt. It seems best, provisionally, to refer the species mentioned below to *Microcyclops* Claus (Syn. *Cryptocyclops* Sars).

While Sars recorded 17 species of *Cyclops* from Tanganyika, Mr. Pask's collection contains only six, of which three appear to be new.

MESOCYCLOPS TENELLUS Sars.

This minute species is not uncommon in Mr. Pask's samples. It has a very striking resemblance to the genus *Oithona* with its slender appendages and very prominent maxillipedes. It is not only the smallest *Cyclops* known, but seems to be the most completely adapted to a limnetic life.

Sars describes the 1st antenna as of 12 joints, but I have been unable to detect more than 10 in any specimen. Joints 3 and 4, and 5 and 6, shown separately in Sars's figure, are fused in my specimens.

EUCYCLOPS RARISPINUS Sars.

This is the commonest species in Mr. Pask's collections, though Sars saw only a single specimen. On the other hand, whereas he found seven species of *Eucyclops*, I have seen only this one species.

MICROCYCLOPS ATTENUATUS Sars.

One female only seen.

MICROCYCLOPS TANGANICÆ, sp. n. (Text-fig. 1.)

Female. Length ·61 mm.

General form as in *C. attenuatus*, but slightly less slender. Last somite of thorax produced on either side and bearing a seta. Genital somite slender. Furcal rami longer than last two somites and about four times as long as broad. Dorsal and lateral setæ rather long and slender. Outer seta about two-thirds as long as innermost seta. Relative lengths of setæ—15 : 57 : 98 : 21.

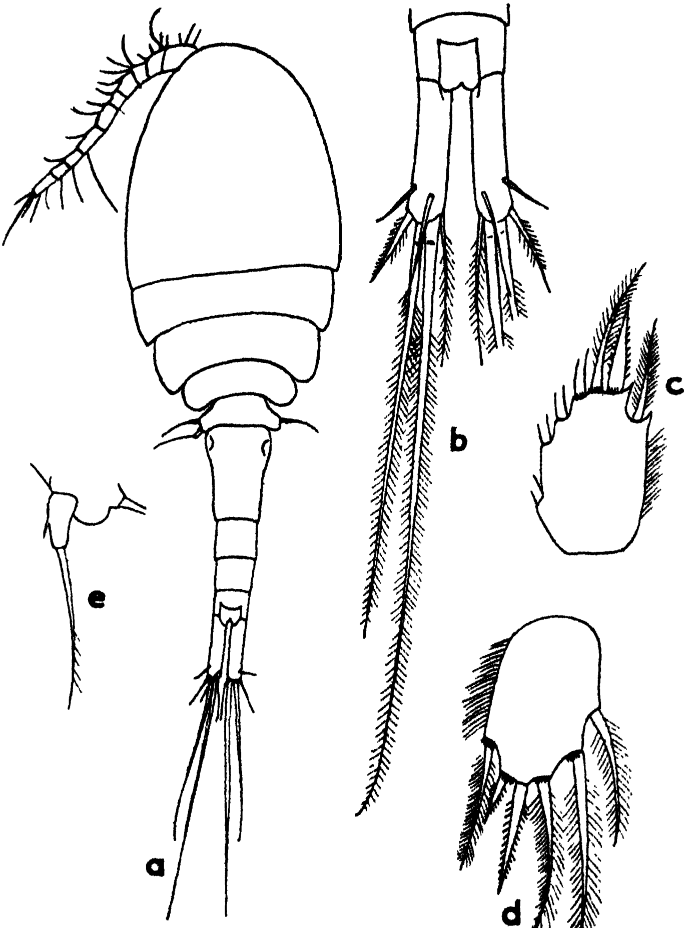
First antenna of ten joints[*], not reaching to end of thorax. Spines on exopods of legs 3, 4, 4, 3. All legs with rami two-jointed. Leg 1 has a seta on the basipod.

Legs 3 and 4 have a comb of short stiff setæ on the inner angle of the basipod. In these legs the second joint of the endopod is broad, the width about two-thirds the length. In each leg there is an outer seta, but in legs 2 and 3 there are five inner and terminal setæ and one stout spine, while in leg 4 there are three setæ and two spines, of which the outer one is less than half the inner. The two distal setæ of leg 4 are much longer than the inner spine. Leg 5 is a small one-jointed rod with a long seta and a very small delicate spine near the base on the inner side. Receptaculum not distinctly visible.

---

[*] Sometimes of 11 joints.

Text-figure 1.



Microcyclops tanganicæ, sp. n.

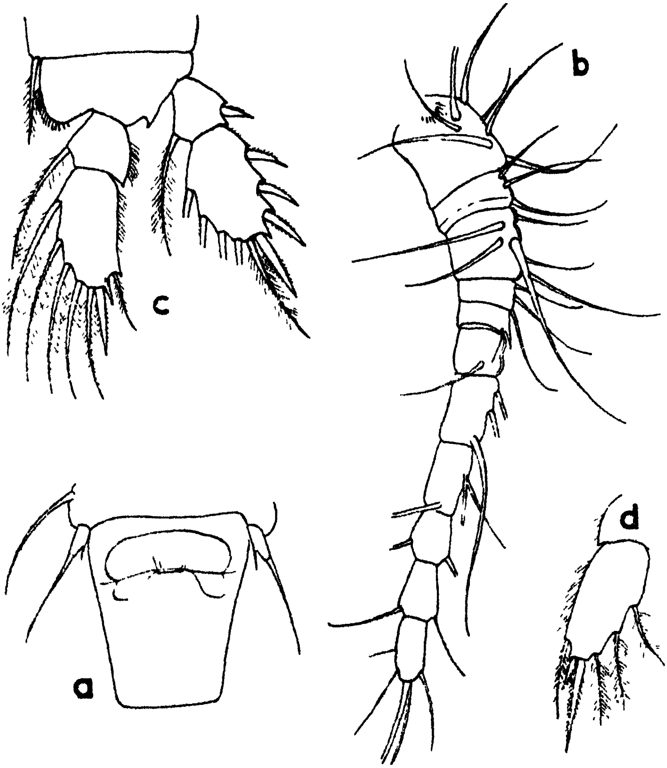
a. Female, dorsal view. *b*. Furcal rami. *c*. Leg 3, 2nd joint of endopod. *d*. Leg 4, 2nd joint of endopod. *e*. Leg 5.

Microcyclops gemellus, sp. n. (Text-fig. 2.)

Resembles the preceding species in nearly all respects, but differs in the following points:—

1. It is somewhat larger, the length being ·78-·8 mm.
2. In legs 3 and 4 the second joint of the endopod is strikingly narrower, the width being about half the length. Also in leg 4 the two distal setæ are much shorter than the terminal spine. The basipod has an inner fringe of stiff hairs which form a conspicuous comb. They are not quite so strong in *M. tanganicæ*.
3. In leg 5 the inner spine is a little longer and stronger.
4. The dorsal seta of the furca is not quite so long. The receptaculum appears to have the form shown in fig. 2 *a*.

Text-figure 2.



Microcyclops gemellus, sp. n.

a. Genital somite, showing receptaculum and leg 5. *b*. 1st antenna. *c*. Leg 3. *d*. Leg 4, 2nd joint of endopod.

These two species and *M. attenuatus* are so much alike that it has been a matter of great difficulty to decide whether to treat them as one variable species or as three. It seems on the whole best to regard them for the present as distinct. *M. attenuatus* differs from *M. gemellus* only in being slightly more slender, with rather more slender furcal rami, and in having no inner spine on leg 5. The endopod of leg 4 is also rather more slender, and the comb on the basipod less developed.

The two species here described are easily distinguishable by examination of the endopod of leg 4. Sars found five species related to *M. varicans* in Tanganyika. It may be that all are derivatives, under the peculiar species-forming influence of the lake, of *M. varicans*, which is common in Lake Victoria.

PLATYCYCLOPS OLIGARTHRUS Sars.

I have seen three specimens of this species which agree well with Sars's description, though differing slightly in the rather shorter furcal rami and in the structure of their setæ. The second seta is not blunt-ended as shown by Sars, and the inner (4th) seta is slender and not spiniform. The sixth leg of the male is unusually well developed (text-fig. 3 *f*).

PARACYCLOPS COPERES, sp. n. (Text-fig. 3.)

Female. Length ·6 mm.

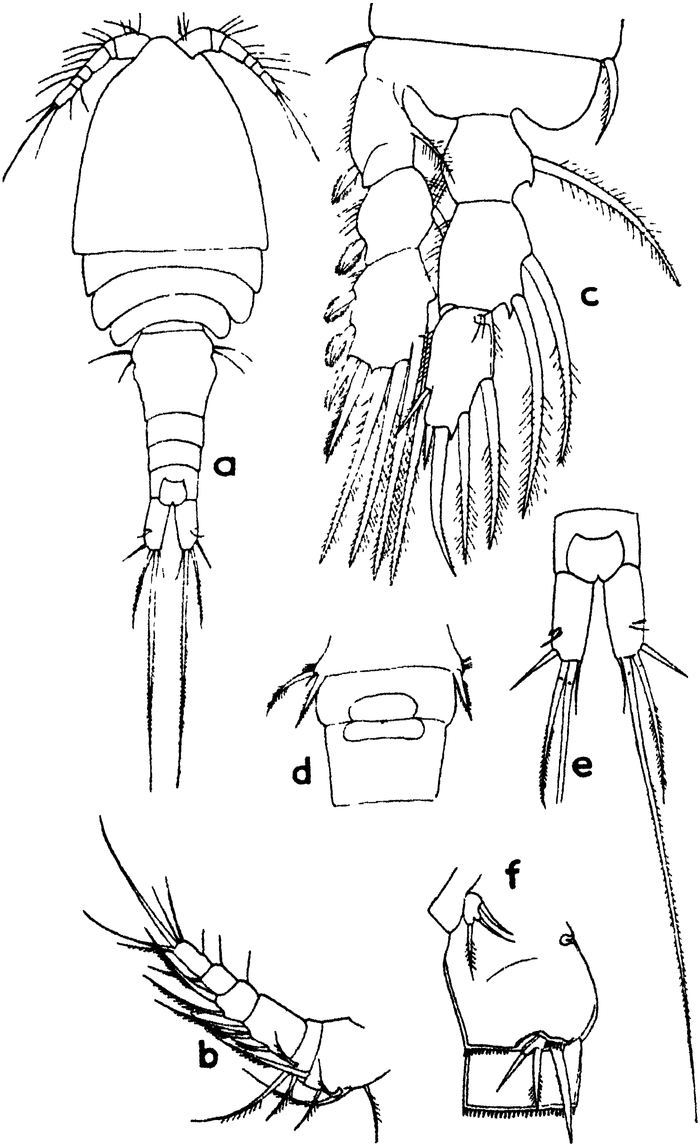
Body rather flattened, thorax narrowed in front. Furcal rami short and thick, little more than twice as long as broad. Lateral seta small, inserted on dorsal surface. In front of it is a short transverse row of small spines. Outer seta spiniform, about the same length as the inner seta. Second seta only one-third the length of the third, or longest, seta.

First antenna short, six-jointed, with numerous coarsely hairy setæ. Legs with rami three-jointed. The outer spines of the exopods have broad, fringed, hyaline membranes. Fifth legs obsolete, represented only by two strong spines springing from the outer angle of the fifth thoracic somite, and a small seta between them. Receptaculum apparently as indicated in fig. 3 *d*.

The species is particularly characterised by the great reduction of the fifth legs and the broad hyaline margins of the spines. Such a form of spine is commonly found in Cyclopoida (e.g. *Euryte*), but is very rare in *Cyclops*. It is curious that so rare a character should be found also in another species from Tanganyika —*C. euacanthus* Sars.

A single female only was found in bottle 511 F—a plankton sample taken from a boat.

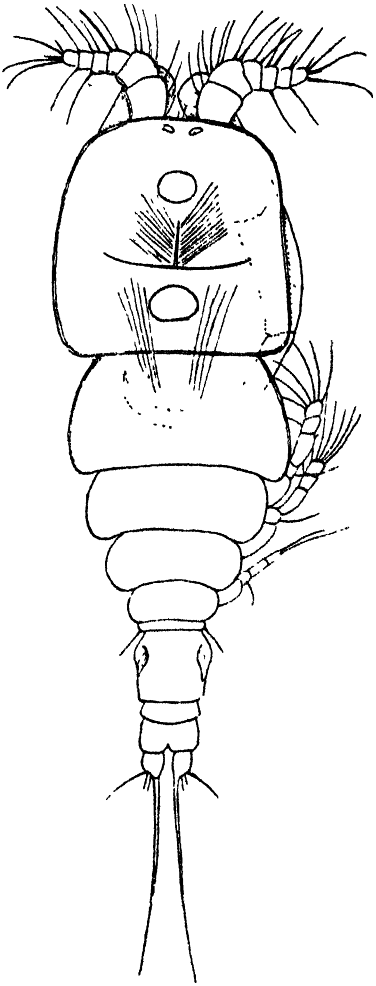
Text-figure 3.



Paracyclops coperes, sp. n.

a. Female, dorsal view. *b.* 1st antenna. Some of the setæ on joint 1 omitted. *c.* Leg 4 from behind. *d.* Genital somite and leg 5. *e.* Furcal rami. *f. Platycyclops oligarthrus* (Sars). Genital somite of male, side view, showing legs 5 and 6.

Text-figure 4.



Ergasiloides macrodactylus Sars.

Free-swimming female of ·8 mm., showing well-developed 2nd abdominal somite.

ERGASILIDÆ.

ERGASILOIDES Sars.

Prof. Sars found in Mr. Cunnington's plankton samples a few specimens of the free-swimming stages of parasitic Copepods for which he established this genus. It differs mainly from *Ergasilus* in having two somites in the abdomen of the female and three in

the male. In some of Mr. Pask's collections Ergasilids are numerous, and can be referred with certainty to Sars's two species *E. megacheir* and *E. macrodactylus*; but in all cases an additional abdominal somite is clearly visible in both sexes. This somite is, it is true, very small and not marked by a transverse line, but there is no doubt of its presence. In one specimen which is strikingly larger than the rest (·83 mm.) this somite is fully developed (text-fig. 4). This specimen does not seem distinguishable, except in size, from *E. macrodactylus*. A further difference from Sars's description is that the 1st antenna is always six-jointed, whereas he describes it as of five joints in *E. macrodactylus*. It must be remembered that these are free-swimming stages and therefore not fully mature, and it is possible that the differences between my specimens and those of Sars may be simply a matter of age. The single large female referred to may be a further and final stage in the development of *E. macrodactylus*. The difference with regard to the abdominal somites does not invalidate the genus, since in true *Ergasilus* there are four in the female and five in the male.

Sars's third species, *E. brevimanus*, appears to be a still younger stage of *E. megacheir*. I have seen specimens agreeing with his description, but in all cases they were obviously immature. The conclusion that this is an immature form is borne out by the reduction of the joints of the exopodites of the legs and also by the form of the furcal setæ, since it is characteristic of the Ergasilidæ that the long setæ of the furca should be forked in early stages. Sars's figure of the abdomen does not show the characteristic genital opening of the mature, or nearly mature, female.

HARPACTICOIDA.

DIOSACCIDÆ.

SCHIZOPERA Sars.

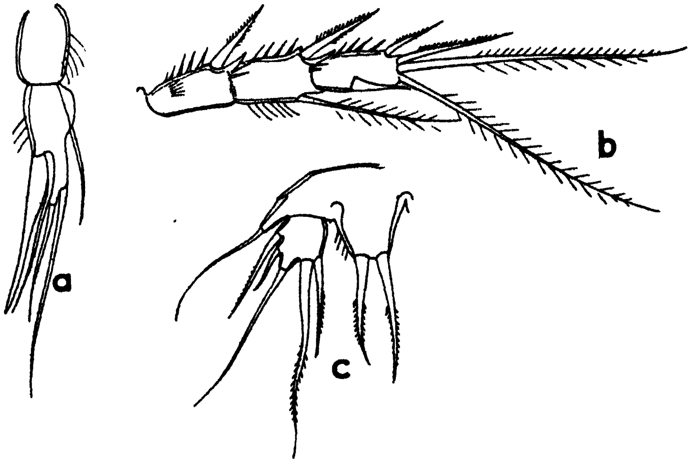
The genus *Schizopera*, founded by Sars in 1905 for a species taken in the Chatham Islands (*S. longicauda*), differs so little from *Amphiascus* that Prof. Sars himself was later inclined to abandon it. The discovery, however, of eight new species in material from Tanganyika (1909) led him to revive the genus. Close as it is to *Amphiascus*, the genus is certainly distinct and has a remarkable distribution. *S. longicauda* has been found to occur in the Baltic region at Oldesloe, the mouth of the Weser, and at Griefswald, while Sars also found it in material from the Birket el Kurun in Egypt. It is also recorded from Lake Elton in S. Russia. *S. jugurtha* Blanch. & Rich. is recorded from Algeria, Turkestan, and New Guinea, while another species, *S. compacta* De Lint, occurs in the Zuider Zee. With these exceptions the genus is confined to Tanganyika, and it is rather remarkable that it has not been found in the Caspian Sea. It contains species of enormously wide distribution, and is characteristic of inland waters of moderate salinity. Though it is a genus of marine type, its presence in Tanganyika is no evidence for a marine connection for the lake.

SCHIZOPERA CONSIMILIS Sars. (Text-fig. 5.)

Not uncommon in Mr. Pask's collections.

The male, which was not seen by Prof. Sars, differs from the female in the construction of legs 1, 2, and 5. Leg 1 is the same as in the female, with the exception that there is a large spine on the coxopod. Leg 2 has the endopod modified. It is two-jointed, the first joint without a seta and the second with two outer setæ, one small terminal seta, and a strong inner spine. A slender seta springs from the same point as the inner spine and is closely apposed to it. Leg 3 was to some extent modified in the specimen examined, the third joint of the exopod having a short stout inner spine.

Text-figure 5.



Schizopera consimilis Sars. Male.
a. Leg 2, endopod. *b*. Leg 3, exopod. *c*. Leg 5.

Leg 5 has two setæ on the inner process of the basal joint. The second joint is as wide as long and has five setæ. The leg formula of the female is as follows[*]:—

	Exopod.	Endopod.
Leg 2	0—1—0, 1, 3	0—1—1, 2, 1
Leg 4	0—1—0, 1, 3	0—1—0, 2, 1

---

[*] For the use of such formula see Gurney 1927, Trans. Zool. Soc. xxii. p. 502.

SCHIZOPERA INOPINATA Sars.

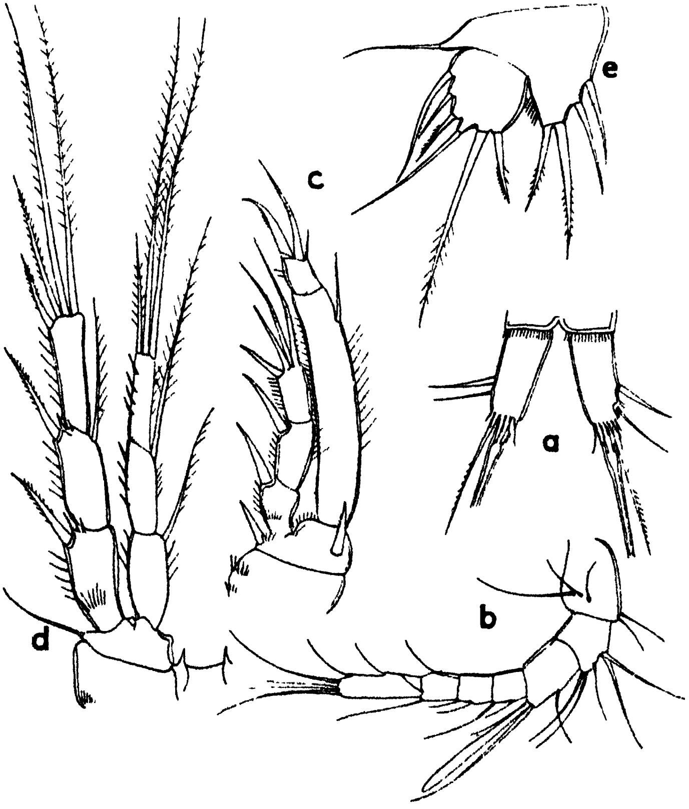
The shape of the second joint of leg 5 is a little more elongated than in Sars's figures, and the relative length of the setæ not quite the same. Also the abdomen, and particularly the last somite and furcal rami, is covered with very minute hairs. These hairs are only visible with difficulty.

A few skins and an incomplete specimen in one sample.

SCHIZOPERA ROTUNDIPES, sp. n. (Text-fig. 6.)

Female. Length ·47 mm.

Text-figure 6.



Schizopera rotundipes sp. n.

a. Furcal rami, ventral. *b*. 1st antenna. *c*. Leg 1. *d*. Leg 4. *e*. Leg 5.

Somites 3 and 4 of abdomen with fine hairs on ventral surface and with a posterior ring of hairs.

Furcal rami long and narrow, the length about twice the greatest width. Outer terminal seta about one-third the length of the median seta, which is about five times as long as the furcal ramus.

First antenna of seven joints; lengths of joints as follows:—

1	2	3	4	5	6	7
14	8·5	11	6	6	7	15.

Æsthete of joint 4 not reaching to end of antenna.

Leg 1 with endopod two-jointed, the first joint longer than the exopod. Second joint very short, about one-sixth of joint 1.

Legs 3 and 4 with the same formula:—

Exopod.	Endopod.
0—1—0, 1, 3	1—1—1, 2, 1

Leg 5: basal joint with four strong spines, of which the second is the longest. Distal joint nearly round, but width rather greater than length. The six setæ relatively short.

This species very closely resembles *S. ungulata* Sars, but differs from it in the form of the furcal rami and particularly in that of leg 5.

In addition to these three species a fourth, which apparently represents a distinct and rather striking species, is present in one of the samples, but is very rare, and only empty skins were found. These specimens seem to be not fully mature, since the second joint of leg 5 is not distinct and the receptaculum seminis is not traceable. On the other hand, the swimming-legs are fully formed, and are remarkable for the presence, in the fourth pair, of a large bulbous swelling at the base of the two terminal setæ of the endopod.

VIGUIERELLIDÆ.

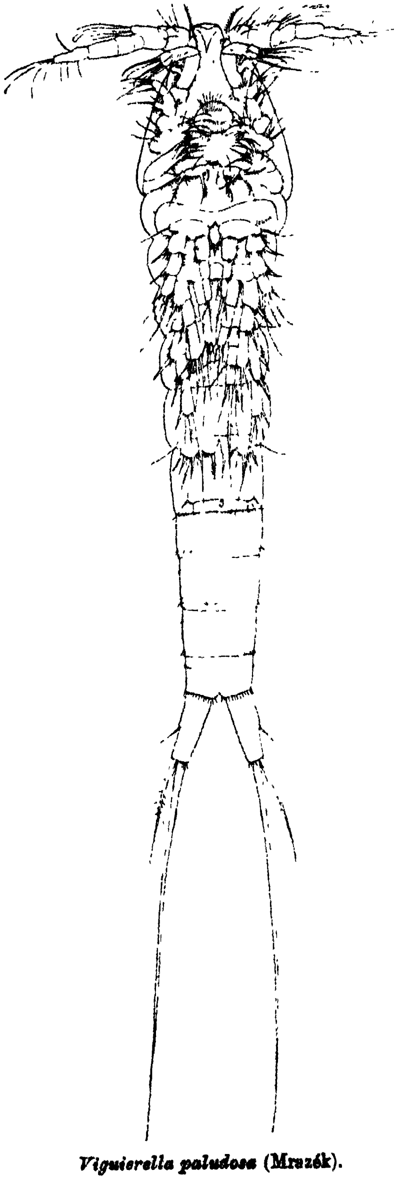
VIGUIERELLA PALUDOSA (Mrazék). (Text-figs. 7 & 8.)

Two specimens of this remarkable species were found in one of Mr. Pask's tubes, one male and one female. These two specimens agree in all respects with Mrazék's description with the following exceptions:—

1. The shape of the fifth legs in both sexes is not quite the same, though the general agreement is very close.
2. The first joint of the first antenna in the female has a feathered seta as in *V. cœca* Maupas.
3. While the mandible palp and the first maxilla agree exactly with Mrazék's figures, there appears to be considerable disagreement in the structure of the second maxilla and maxillipede. Unfortunately these can only be seen in the male, and not sufficiently well to allow of a very positive statement. The maxillipede appears as a very small appendage lying transversely and directed outwards, consisting of three joints, the third very small and bearing stout feathered setæ.

Apart from this difference, which, if it could be verified, would

Text-figure 7.



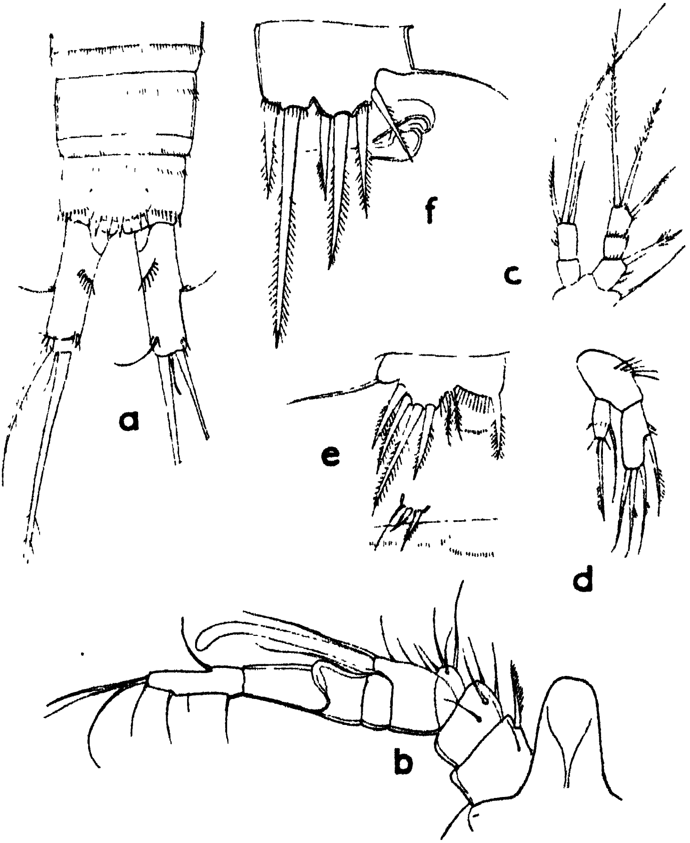
***Viguierella paludosa* (Mrazék).**

Male, ventral view. The 4th legs are hidden beneath the 3rd pair. Endopod of leg 3 omitted on right side.

amount to an important distinction, I do not consider it possible to separate the Tanganyika form from Mrazék's species.

The history and distribution of the genus have been well summarised by Chappuis (1916). It consists now of four species—*V. cæca* Maupas, *V. paludosa* Mrazék, *V. fodinata* Ziegelmeyer,

Text-figure 8.



Viguierella paludosa (Mrazék).
a. Furcal rami, female. *b.* 1st antenna, male. *c.* Leg 4, female. *d.* Mandible palp. *e.* Leg 5, male. *f.* Leg 5, female.

and *V. chappuisi* Delachaux. *V. paludosa* was originally taken in damp moss in Bohemia, and has since been found by Borutzky in Russia (Kossino) and by Chappuis in North America. It should, however, be pointed out that Borutzky's figure of the fifth leg of the male differs a good deal from that of Mrazék, and agrees closely with that of *V. chappuisi.*

As regards systematic position, all authors have followed Mrazék in placing the genus in the family Longipediidæ, but without, so far as can be seen, any reason other than the great reduction of the maxillipede. The Longipediidæ in Mrazék's sense would correspond to the whole of Sars's Achirota. Now, the subdivision of the Harpacticoida into Achirota and Chirognatha is a matter of convenience, but can hardly be accepted as a satisfactory division on phylogenetic grounds. The Achirota are an assemblage of families probably by no means closely related, and the Misophriidæ should certainly not be included. The main character which they have in common is the non-prehensile maxillipede; but this is not, in itself, distinctive. Among the Chirognatha, for instance, *Stenhelia palustris* has a reduced and non-prehensile maxillipede, while other species of the genus have a normal prehensile appendage. In *Ceyloniella* (*Ceylonia* Scott), again, this appendage is reduced to a form very closely resembling that of *S. palustris* and not unlike that of *V. paludosa* as figured by Mrazék. Another example is *Pseudomesochra parvula* Gurney (1927), in which the maxillipede is much reduced and can hardly be described as prehensile. The structure of the maxillipede cannot then be regarded as evidence of the relationship of *Viguierella* to the Longipedildæ or any other Achirote family. From the Longipediidæ it differs very greatly in the structure of both pairs of antennæ and the mandible, while it also differs from the Ectinosomidæ (to which it has otherwise a resemblance in general form) in the structure of the five pairs of legs.

The genus should, in my opinion, be included in the section Chirognatha, but it is impossible to refer it to any existing family. There is some resemblance to *Ceyloniella*, but it seems best to establish a new family (Viguierellidæ) for its reception, and to place it in the neighbourhood of the Ceyloniidæ and Cylindropsyllidæ. The family might be thus defined:—

VIGUIERELLIDÆ, fam. n.

Harpacticoida of slender form, without distinction between thorax and abdomen; first leg-bearing somite separated from head; rostrum large and broad. Second antenna with outer branch one-jointed; mandible palp two-branched; maxillipede reduced and non-prehensile. First three pairs of legs with both branches three-jointed, fourth pair much smaller and with endopod two-jointed Fifth legs with second joint fused with first. Male with first antenna relatively little modified and third pair of swimming-legs quite unmodified. The second pair may be modified or not. Eggs laid free and not carried in egg-sacs.

LIST OF REFERENCES.

1916. CHAPPUIS, P. A.—*Viguierella cæca* Maupas. Rev. Suisse Zool. xxiv. p. 521.

1920. CUNNINGTON, W. A.—The Fauna of the African Lakes. A Study in Comparative Limnology, with Special Reference to Tanganyika. Proc. Zool. Soc. London, 1920, p. 507.

1927. KIEFER, F.—Versuche eines Systems der Cyclopiden. Zool. Anz. lxxiii. p. 302.

1909. SARS, G. O.—Report on the Copepoda. Zoological Results of the Third Tanganyika Expedition. Proc. Zool. Soc. London, 1909, p. 31.

1918. SARS, G. O.—Crustacea of Norway, vi. Cyclopoida.

17. The Mallophaga of Sand-Grouse.

By JAMES WATERSTON, B.D., D.Sc., F.Z.S.

(Offered for publication by permission of the Trustees of the British Museum.)

[Received April 12, 1928: Read May 1, 1928.]

(Text-figures 1-10.)

Up to the present little has been recorded regarding the insect parasites of the order Mallophaga occurring upon Sand-Grouse (Pteroclidæ). In 1870 Rudow described a Philopterid species, *Nirmus alchatæ*, from *Pterocles alchata*, and more recently Bedford (1920) brought forward a new Menoponid, genus and species, having as its host a South African member of this peculiar family of birds. But though the two main divisions of the Mallophaga were thus represented amongst the parasites of Sand-Grouse, further investigation seemed desirable, and, accordingly, about two years ago I examined a large proportion of the collection of Sand-Grouse skins in the British Museum, and have embodied the results in the present paper.

The method of examination may be briefly described. The skins were gently ruffled by hand above a sheet of paper until the whole body had been gone over. The stroke—an upward one, delivered by the tips of the fingers only—should be short and light, and passing from the tail to the head of the bird. Next, holding the skin back upwards, the wings are separately slightly extended, and a series of taps given mainly above the secondaries. The tips of primaries and secondaries should, during this operation, be kept deflected to prevent the parasites falling outside the sheet. In this way, by repeated tapping, insects deeply embedded in the plumage may be gradually dislodged. As the result of the treatment just described, some 50 skins yielded an average of rather over two Mallophaga. This may seem a low figure when one remembers that in life practically all birds are more or less heavily parasitised. But it should be noted that many of the skins searched were over forty years old; that a large proportion had been repeatedly handled and cleaned; and that in some instances the skins had been made down, though originally mounted. Nevertheless, the parasites could still be found, though sometimes with broken appendages. As an extreme instance one might cite an example of *Syrrhaptes paradoxus*, acquired by the Museum in 1842, which yielded after 85 years, five examples of the parasite peculiar to this host.

The preparation of Mallophaga collected in the manner just described is a simple one. The specimens, dropped into a test-tube partly filled with a 10-per-cent. solution of KOH, are placed in a bath on an electric heater. In about ten minutes they sink to the bottom of the tube, whose contents are then poured into a watch-glass, and the caustic pipetted off. Next, cover with acetic acid (80 per cent.). The crop can then be drawn out by a slit made transversely in the region of the second sternite, and its contents, with those of the abdomen, evacuated by manipulating with two fine, blunted needles. Stain at this point with a drop of Ziehl's carbol Fuchsin, and wash out if necessary in fresh acid, transferring thereafter to a mixture of equal parts glacial acetic acid and clove oil, and mount finally from pure clove oil. The staining should be light, leaving only sufficient colour to show up the membranous areas and thinner chitinisations. Over-staining can be corrected by soaking the preparation in tap-water. The crop (♂ ♀) and the male genitalia (ventral side up) should be mounted separately. Their dissection is most easily effected while the specimens are in the acetic-clove-oil stage.

Students of the Mallophaga are well aware of many instances of the occurrence, on a series of allied birds, of a parallel series of extremely similar parasites differing *inter se* mainly in apparently trivial details of dimensions. *Degeeriella furva* (various Waders), *Philopterus lari* (Laridæ), and *Philopterus subflavescens* (Passerines) sufficiently indicate the type of series under discussion. Such names may, on careful analysis, prove to cover many species, or one species or a series of subspecies. Further, when the presence of several *entomological* species can be established and their respective host species are accurately worked out, it has been found in many cases that these separate groups of host species are recognized as *ornithological* genera. An additional interest in the present investigation has been its possible bearing on the systematics of the hosts themselves.

The material collected comprised a Menoponid (one species) and several species of the Philopterid genus described below.

The full list of hosts and parasites is as follows (hosts arranged alphabetically within each genus; * = straggler):—

Genus Syrrhaptes Gould.

paradoxus Pall.
    Syrrhaptœcus bedfordi.

tibetanus Gould.
    Syrrhaptœcus tibetanus.

Genus Pterocles Temm.

alchata Linn. and var. *caudacutus* Gmel.
    Neomenopon pteroclurus.
    Syrrhaptœcus alchatæ.

namaquus Gm.
    Neomenopon pteroclurus.
    Syrrhaptœcus brevifrons.
    Syrrhaptœcus digonus.

senegalensis Licht. and var. *orientalis* Hasselq.
Syrrhaptœcus falcatus. ✗

senegallus Linn.
Syrrhaptœcus sp. "*mitratus*" section.
**Syrrhaptœcus falcatus.*

Genus Eremialector W. Sclater.

bicinctus Temm.
Syrrhaptœcus declivis.

burchelli W. Sclater.
None found.

coronatus Licht.
Syrrhaptœcus brevifrons.
Syrrhaptœcus mitratus. ✗

decoratus Cab.
Syrrhaptœcus sp.

gutturalis Smith and var. *saturatior* Hart.
Syrrhaptœcus uncinosus.

indicus Gmel.
Syrrhaptœcus angulatus. ✗
**Syrrhaptœcus alchatæ.*

lichtensteini Temm.
None found.

orientalis Linn.
Syrrhaptœcus pallasi. ✗

personatus Gould.
Syrrhaptœcus obtusus

quadricinctus Temm. var. *lowei* C. Grant.
Syrrhaptœcus brevifrons.
Syrrhaptœcus excisus.

In the British Museum 'Hand-List of Birds,' vol. i. pp. 50–51 (1899), there are enumerated 17 species of Pteroclidæ distributed in three genera. As however, one of these species (*Pterocles pyrenaicus* Seebohm) is now regarded as a race of *P. alchatus*, we may take the accepted number of living Sand-Grouse as sixteen. There are, of course, several subspecies or races which would have to be included in a complete systematic catalogue of the group, but host subspecies are for our present purpose irrelevant. In this paper parasites of fourteen of the above host species are dealt with, but on two species, *Eremialector burchelli* W. Sclater and *Eremialector lichtensteini* Temm., nothing was found. In the case of two of the remaining host species the evidence obtained is unsatisfactory, since on *Eremialector decoratus* Cab. only a female *Syrrhaptœcus* was taken, while of the two species found on *Pterocles senegallus* Linn., one was evidently a straggler while the other was represented by a male too damaged for exact determination. Making these allowances, however, we are left with material from three-fourths of the known hosts on which to base any general conclusions reached. We may ask the following questions:—(1) Do the parasites of Sand-Grouse throw any light on the phylogeny of their hosts as a whole? (2) Do they give us any clues as to the natural divisions within this group of hosts or the inter-relation of the host species?

1. On the first point the evidence is fairly definite. Though *Syrrhaptœcus* is, so far as we know, confined to the Pteroclidæ, it has very obvious affinities with *Lagopœcus*, of which species are found on the genera *Lagopus*, *Lyrurus*, *Tetrao*, and *Lophophorus*. The genus *Lagopœcus*, however, seems to be more primitive, *e.g.* in no species is the male furnished with an appendix on the third joint; the male genitalia are simpler, lacking the lower plate and its elaborate folds; the pleurites have no complicated head; the post-spiracular bristle is present up to the seventh tergite (in *Syrrhaptœcus* up to the fifth). Apart from these differences, *Syrrhaptœcus* and *Lagopœcus* agree closely in facies and structure, and both are related to *Lipeurus* (s. str.), which is specially characteristic of gallinaceous birds.

Syrrhaptœcus has not, in my opinion, any close affinities with any of the Philopteridæ found on Pigeons (Columbidæ), though the latter family also, judged by its parasites, is related only to the galline group. Sand-Grouse and Pigeons must stand rather apart within this complex, and the position of the first-named would appear to be between the Grouse and the Pheasants.

2. The high degree of specialisation reached within the genus *Syrrhaptœcus* permits only one general deduction, viz., that the host species must, as species, be of considerable antiquity. One would naturally infer also that *P. alchata* and *S. tibetanus* are somewhat isolated birds.

The *Syrrhaptœcus* spp. found on the genera *Syrrhaptes* and *Pterocles* are more highly differentiated, while the majority of those on *Eremialector* are closely similar, and, judging by analogy, one would expect to find a like relation holding of their hosts, *i. e.* that *Eremialector* is the most compact genus of the three. In the genus *Lagopœcus* the species, so far as is known, correspond to host genera. If the same relation held between the Pteroclidæ and their parasites, we should require about ten genera for the distribution of the hosts. Genera, however, are so much a matter of convenience that it would perhaps be unwise to stress this suggestion. At the same time it is worth noting that Austin Roberts [Annals of Transvaal Museum, viii. pp. 195–6 (1922) and x. pp. 95, 123–4 (1924)] has drawn attention to characters by which the presently-admitted genera of the Pteroclidæ may be further subdivided *.

SYRRHAPTŒCUS, gen. n.

Small Philopteridæ (males 1·5–2 mm., females 2–2·5 mm.) with a Lipeuroid facies, found solely on various Sand-Grouse (Pteroclidæ), showing the following combination of characters:—

♀. Head circumfasciate; parabolic to sub-ogival in front of the antennæ: fore, and hind head subequal in length; temples gently swollen behind the eyes and slightly convergent posteriorly; occiput varying from nearly straight to gently concave or subsinuate; oral fossa triangular with rounded angles; trabeculæ shorter and movable; neither signature nor defined clypeal suture present.

Chætotaxy of Head.—Clypeal hairs (lateral) 4, 4 with 3, 3 (ventral) between the sides of the oral fossa anteriorly and the inner edge of the marginal band; the usual lateral (2, 2) and trabecular (1, 1) bristles present. One long hair at eye, one at middle of temple, and another before the postero-lateral angle; minute spinose bristles occur singly at postero-lateral angle and between the long temporal hairs. On upper surface the usual median pair of short fine bristles on clypeus and a second pair (1, 1) at the anterior ends of the ocular bands. Hind head and occiput otherwise bare.

Thorax.—*Pronotum* transverse; one postero-lateral bristle somewhat remote from the angle. *Mesometanotum*; *Mesonotum* short, parallel-sided. *Metanotum* broadly angled over abdomen, with sides divergent, the pleurites stout and extending beyond the tergite postero laterally. *Chætotaxy*: five bristles normally on each side along the posterior edge at the sides, the two outer bristles finer, the others in clear pustular bases.

Abdomen.—T. I. (=T. I.+T. II. fused) with divergent sides and posteriorly concave. Pleurites strongly thickened, with large re-entrant "heads." From the inner (posterior) end of the head a ventral chitinous strut always connects up with the marginal thickening. The corresponding dorsal strut present or absent. Thus from above the "head" of the pleurite is more or less distinctly perforate. (Text-figs. 9, 10.)

Tergites (I.–VIII.) medianly and longitudinally divided, secondary (*e. g.* intersegmental) chitinisations slight, a chitinous ridge between the post-spiracular hair and margin. Posterior edge of valve varying in outline from transverse to parabolic, with a single row of minute marginal bristles and a second row (in most species) developed adbasally, *i. e.* laterally. Chætotaxy (see below, p. 352).

Legs.—Fore tibia longer than, mid tibia subequal to, hind tibia shorter than, their respective femora.

♂. Similar to the female, but with a narrower head and shorter body. Genitalia: basal plate from one and a half to two and a half times as long as the mesosome and widest distally (posteriorly). Paramers simple, knife or sickle-shaped, fitting closely to the sides of the mesosome when at rest, and generally with a thickened basal collar. Mesosome much flattened, consisting of two thin chitinous plates, the upper always longer. From the lower (*i.e.* from the ventral aspect) projects the fine tubular intromittent organ.

---

* *Cf.* also Bowen, Amer. Mus. Novit. No. 273, pp. 1–22, 1927.

Note. The upper plate represents the fused endomers, and the lower equals apparently the sac and telomers. Only in one species (*alchatæ*) does any part of the sac remain membranous.

Abdominal Chætotaxy (♂, ♀).—A complete examination of the specimens collected shows that all the elements of the chætotaxy (save some of the minutest bristles on the head and genital plate, ♀) are perfectly definite in number and disposition. Further, the sexes differ only in minor details of the terminal segments. The arrangement of the bristles, hairs, etc., appears in the main to be a generic character, but in some of the species extra elements are present in the rows. The normal chætotaxy is given under the description of *S. uncinosus*, sp. n., divergences being noted under the species respectively concerned.

SYSTEMATIC NOTES.

Throughout the Philopteridæ generally, the most useful specific characters are to be found in the male genitalia. So far as possible, therefore, males have been selected as types in the following descriptions. Though the male characters appear to be very precise, it is essential that identification should be attempted only from the dissected apparatus. In whole mounts the characters of the mesosome may be either distorted, obscured, or foreshortened. Only in the "*mitratus*" section can any difficulty be felt in determining male *Syrrhaptœcus*.

The separation of the females is, however, an extremely critical matter in the species with a narrower head, *i.e.*, where the C. I. drops below ·80. Valuable characters in the head (♀) are (1) the general shape and (2) the absolute width. Most useful, too, is the ratio between the breadth and length —the head index just referred to. The normal range of specific variation of this ratio in *Syrrhaptœcus* is from ·01 to ·03, though occasionally it may reach ·05.

The C. I. may be very expeditiously ascertained by the use of a slide-rule. If at the same time the inner tube of the microscope is adjusted so that with the low power 100=1 mm. the gross measurements can be read off at once, while by noting, under the high power, the number =·1 mm., the measurements of the more minute details may again be read from the slide-rule. No arguments, fortunately, are required to prove the importance of such detailed measurement in descriptions of Mallophaga; but to carry this, as has lately been done, to four or five decimal places of a millimetre seems fantastic. In my opinion, no figure beyond the second decimal has critical significance. In the ovigerous female the dimensions of the abdomen are markedly affected.

In the descriptions of the new species now made the following contractions are employed:—

C. I. Head index (breadth : length).
l. Total length. b. Greatest breadth (*i. e.*, of abdomen on the 4th (5th) segment). b. t. Breadth of thorax.
b. h. Breadth of head. l. h. Length of head.
G. A. Genital apparatus (♂) (ædeagus), length measured when dissected. b. p. Basal plate (length).
P. Paramer (length). p. Paramer (length : breadth).
Pen. l. Length of tubular intromittent organ. m. Mesosome (length). T. Tergite. Pl. Pleurite. S. Sternite.
Letters A, B, C, D, etc., individuals measured.

The measurements are in millimetres, except in the case of the C. I. and p, which are *ratios*; in the former reduced, the denominator being 1.

In the abdomen Tergites I. and II. are fused and the corresponding sternite is S. II.

SYRRHAPTŒCUS BREVIFRONS, sp. n. (Text-figs. 1 *b*, 7.)

Male.—C. I., 1·02; l., 1·45; b., ·55; b. t., ·35; b. h., ·42; l. h., ·41; G. A., ·30; b. p., ·22 : p., ·8; P., 7 : 1; pen. l., ·046; mesosome, ·12.

Female.—C. I., 1·07; l., 2·04; b., ·70 : b. t., ·50; b. h., ·52; l. h., ·48.

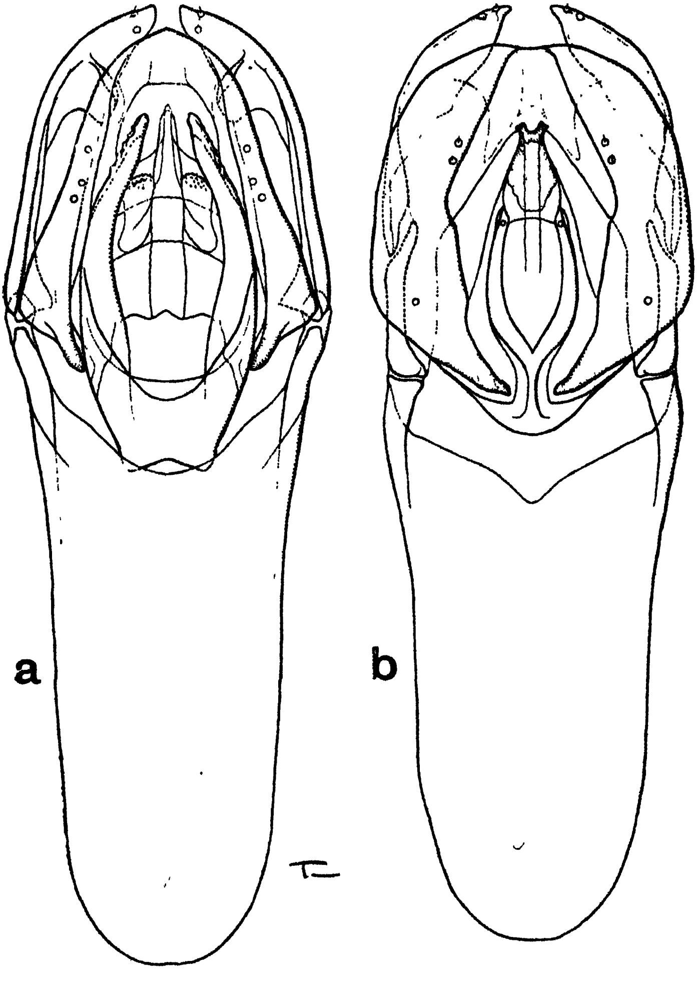
In crop more than one row of toothed plates (more primitive) (text-fig. 7 *b*).

Valve transverse, 6–7 : 6–7.

Chætotaxy (abd.). *Female.*

	T.	Pl.	S.
I. .. .	1, 1	0	—
II.	3-4, 3-4	0	1, 1
III.	1, 4–5, 4–5, 1	0	2, 2
IV.	1, 4, 4, 1	1	2–3, 2–3
V.	1, 4, 4, 1	1	2–3, 2–3
VI.	1, 4, 4, 1	2	2–3, 2–3
VII.	0, 3, 3, 0	2	2, 2
VIII.	0, 3, 3, 0	4	1, 1
IX.	0	2/2	—

Text-figure 1.

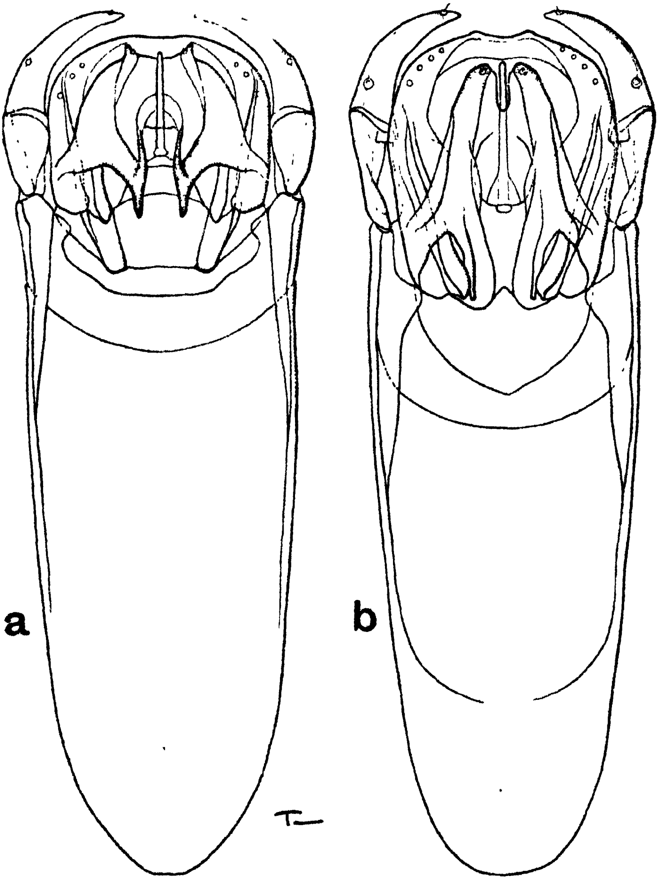


Male genitalia of (a) ***Syrrhaptœcus alchatæ*** **Rud. (b)** ***Syrrhaptœcus brevifrons*** **Waterst.**

Host, ***Eremialector*** *coronatus* Licht. ♂, **Holotype,** Muscat (Mills Coll.).
" " *quadricinctus* Temm. ♀, **Allotype,** Sudan, Kordofan, El Obeid, 26. viii. 1909 (W. G. B. Halked Coll.).
" *Pterocles namaquus* Gmel. ♂. 3 ♀, Rustenburg Dist., Transvaal, 3. ix. 1917 (Bedford Coll.).

This is the most easily recognized member of the genus, being at once separable, even without mounting, by the broad rounded head (text-fig. 7 *a*). In consequence of the shortening of the forehead, the oral groove has become transverse and somewhat atypical for the genus. The legs are also longer and more robust. In the abdomen the post-spiracular hair is present on T. VI., though not on T. VII. or T. VIII.

Text-figure 2.



Male genitalia of (a) *Syrrhaptœcus falcatus* Waterst. (b) *Syrrhaptœcus bedfordi* Waterst.

In the male genitalia the paramer (text-fig. 1 *b*) appears to be free only apically, and the ventral plate of the mesosome is very peculiar.

In the female the valve is transverse.

The suggestion has been made to me that these differences, in conjuction with the apparently wider host range of this species, are of generic value. Perhaps the creation of a subgenus might be justified, but at present it seems more important to emphasise the essential unity of these Sand-Grouse Philopterids.

It is not impossible that *S. brevifrons* represent a common ancestral parasite of the group from which have come the various species with a more limited host attachment.

SYRRHAPTŒCUS BEDFORDI, sp. n. (Text-figs. 2 *b*, 9 *c*.)

Male.

	A.	B.	C.	D.	E.
C. I. ...	·84	·86	·86	·84	·84
l. . .	1·51	1·57	1·5	1·58	1·59
b.	·50	·52	·47	·5	·54
b. t. ...	·31	·32	·31	·31	·32
b. h.	·36	·36	·37	·37	·36
l. h. .	·43	·44	·43	·44	·43
G. A.	·39	—	—	·43	·45
b. p. ..	·29	—	—	·33	·35
P. ...	·1	—	—	·1	·1
p. . .	6 : 1	—	—	6 : 1	6 : 1
pen. l. .	·064 (bent)	—	—	·067	·067

Female.

	A.	B.	C.	D.	E.
C. I. .	.86	·87	·87	·86	·86
l.	2·14	2·38	2·05	2.	2·07
b. .. .	·61	·66	·56	·48	·59
b. t.	·37	·42	·36	·35	·38
b.h.	·44	·47	·43	·43	·43
l. h. ...	·51	·53	·49	·50	·50

Chætotaxy normal.

Valve 8–9, 3–4.

Host, *Syrrhaptes paradoxus* Pall. 3 ♂, **Holotype** and **Paratypes,** Tian Shan, Koyssara, 15. i. 1905 (A. Kutzenko Coll.). ♂, 4 ♀, **Allotype,** N. Asia, 1842. ♂, England, Sussex, Lewes, 20. i. 1889 (Brazenor Coll.). ♀ loose in box.

SYRRHAPTŒCUS TIBETANUS, sp. n. (Text-fig. 3 *b*.)

Male.

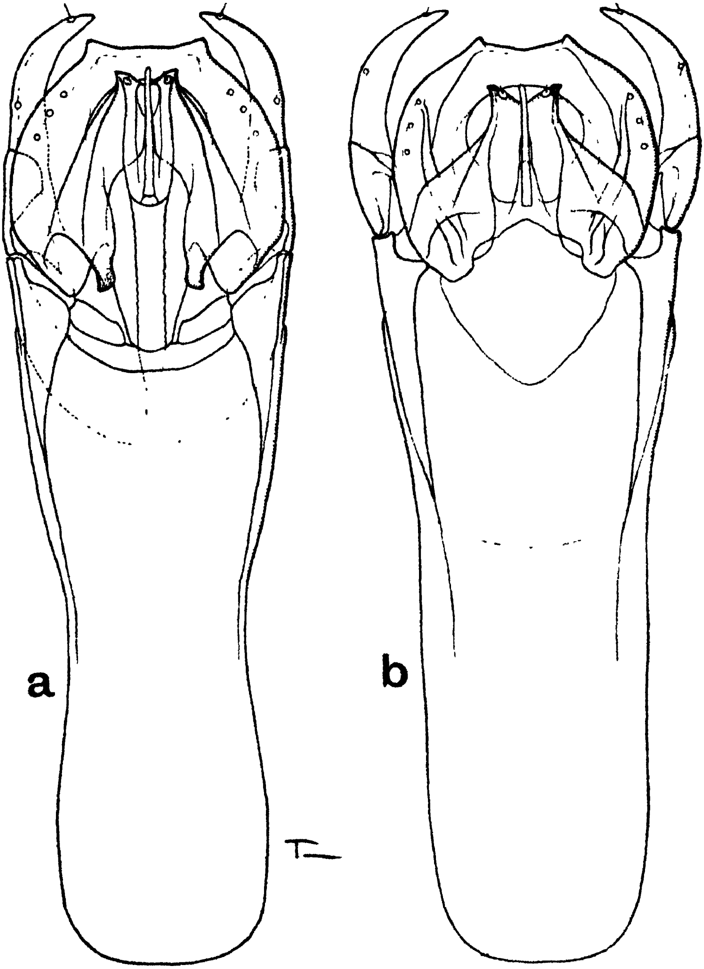
	A.	B.	C.
C. I.	·89	·88	·885
l.	1·94	1·92	1·
b.	·72	·72	·70
b. t.	·45	·46	·45
b. h.	·47	·46	·46
l. h.	·53	·53	·52
G. A.	·58	·57	—
b. p.	·45	·45	—
P.	·13	·13	—
p.	19 : 3	19 : 3	—
pen. l.	·066	·066	—

Female.

	A.	B.	C.	D.
C. I.	·90	·9	·91	·90
l.	2·4	2·31	2·36	2·47
b.	·80	·86	·72	·84
b. t.	·48	·51	·45	·50
b. h.	·53	·54	·52	·53
l. h.	·58	·60	·57	·58

Valve 10–12, 5.

Text-figure 3.



Male genitalia of (a) *Syrrhaptœcus digonus* Waterst. (b) *Syrrhaptœcus tibetanus* Waterst.

Chætotaxy (abd.). *Female.*

	T.	Pl.	S.
I. …………	1, 1	0	—
II. …………	6, 6	0	5–6, 5–6
III. …………	1, 8, 8, 1	1	5–6, 5–6
IV. …………	1, 8, 8, 1	3	4, 4
V. ……… …	1, 8, 8, 1	3	4, 4
VI. …………	0, 7–8, 7–8, 0	3	4, 4
VII. …………	0, 7, 7, 0	3	1–2, 1–2
VIII. …………	0, 6, 6, 0	3	2, 2
IX. …………	0	2/2	0

Host, *Syrrhaptes tibetanus* Gould. 2 ♂, Ladak (Hume Coll.). ♀, Karakorum, 16. vi. 1874. 2 ♂, Thibet, xi. 1877 (L. Mandelli, Hume Coll.). 3 ♂ **Holotype,** 4 ♀ **Allotype** and **Paratypes,** 2 larvæ, Thibet, Khambjong, x. 1903 (Capt. H. J. Walton Coll.). 2 ♂, India, Kashgar (Dr. Bellew—Indian Museum). ♂, ♀ loose in box.

SYRRHAPTŒCUS ALCHATÆ Rud. (Text-fig. 1 *a*.)

Nirmus alchatæ, Rudow, Zeits. f. ges. Nat. xxxv. p. 472 (1870).

Male.

	A.	B. *indicus.*	C.	D.	E.	F.	G.	H.
C. I.	·84	·84	·84	·85	·85	·85	·85	·84
l.	1·58	1·57	1·82	1·74	1·71	1·57	1·63	1·62
b.	·49	·48	·58	·57	·54	·46	·51	·50
b. t.	·35	·37	·41	·40	·40	·36	·35	·34
b. h. ...	·38	·38	·41	·40	·40	·37	·39	·38
l. h.	·45	·45	·475	·47	·47	·44	·46	·45
G. A. . .	·44	·38	·44	—	—	·39	·40	—
b. p.	·30	·25	·30	—	—	·26	·26	—
P.	·14	·13	·14	—	—	·13	·14	—
p.	7 : 1	7 : 1	7 : 1	—	—	7 : 1	7 : 1	—
pen. l. .	·053	·054	·05	—	—	—	—	—

Female.

	A.	B.
C. I. . . .	·90	·90
l.	2·07	2·14
b.	·62	·70
b. t.	·44	·46
b. h.	·46	·48
l. h.	·51	·53

Valve 8, 8.

Chætotaxy (abd.). *Female.*

	T.	Pl.	S.
I.	1, 1	0	—
II.	2, 2	0	1, 1
III.	1, 2, 2, 1	0	1, 1
IV.	1, 2, 2, 1	1	1, 1
V.	1, 2, 2, 1	1	1, 1
VI.	0, 2, 2, 0	2	1, 1
VII.	0, 2, 2, 0	2	2, 2
VIII.	0, 2, 2, 0	4	1, 1
IX.	0	2/2	—

Host, *Pterocles alchata* Linn. and var. *caudacutus* Gmel.

3 ♂, 2 ♀, 2 larvæ, Palestine, Gaza, 20. viii. 1917 (Major A. G. L. Sladen Coll.).

2 larvæ, Bagdad (Loftus Coll.).

3 ♀, Mesopotamia, Bagdad, 23. ix. 1922 (V. S. La Personne—Cox Cheesman Coll.).

♂, Turkestan, Samarkand, 30. v. 1908 (Dr. Carruthers Coll.).
♂, India, Gurgaon Dist., 1. ii. 1883 (W. N. Chill—Hume Coll.).
♂ loose in box. ♂, Zool. Gdns., London.
Also ♂ (straggler) from *Eremialector indicus* Gmel., India, Gurgaon Dist., 2. iii. 1869 (Hume Coll.).

SYRRHAPTŒCUS DIGONUS, sp. n. (Text-figs. 3 *a*, 8 *b*, 10 *c*.)

Male.

	A.	B.	C.	D.	E.	F.	G.	H.	Bedford. I.
C. I.	·80	·775	·77	·79	·775	·77	·78	·78	·80
l.	1·7	1·7	1·67	1·62	1·66	1·56 (imm.)	1·7	1·77	1·75
b.	·46	·43	·44	·43	·43	·42	·42	·45	·46
b. t.	·34	·32	·31	·32	·31	·31	·31	·34	·32
b. h.	·36	·34	·33	·35	·34	·34	·34	·34	·34
l. h.	·45	·44	·43	·44	·44	·44	·44	·44	·43
G. A. . .	·37	·35	—	—	—	—	·34	·36	—
b. p. ..	·27	·26	—	—	—	—	·25	·27	—
P.	·95	·93	—	—	—	—	·9	·9	—
p. ..	8 : 1	7 · 1	—	—	—	—	7½ : 1	7 : 1	—
pen. l. .	·044	·045	—	—	—	—	·042	·046	—

Female.—C. I., ·775; l., 2·1; b., ·56; b. t., ·36; b. h., ·41; l. h., ·53.

Chætotaxy normal.

Host, *Pterocles namaquus* Gm.

From the following localities (S. Africa):—

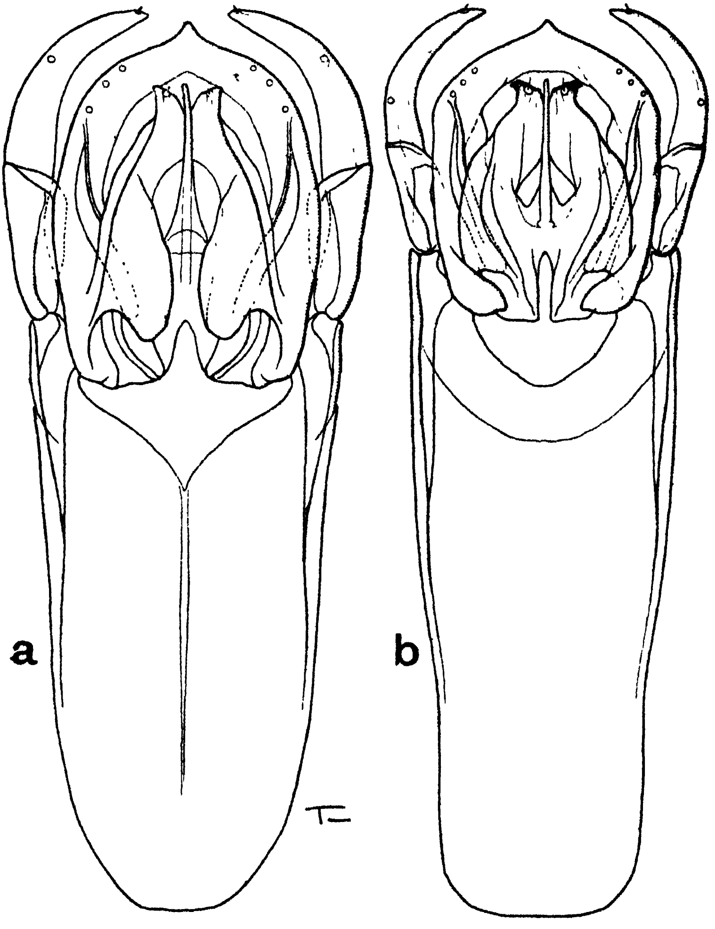
5 ♂, **Holotype** and **Paratype**, Little Namaqualand, Klipfontein, 3100 feet, 12. v. 1903 (C. D. Rudd Coll.). ♂, 24. ii. 1902; 2 ♂, ♀, **Allotype**, 15. v. 1902, Cape Colony, Deelfontein (Col. A. T. Sloggett Coll.). ♂, ♀, 3 larvæ, Rustenburg Dist., Transvaal (Bedford Coll.).

SYRRHAPTŒCUS FALCATUS, sp. n. (Text-figs. 2 *a*, 10 *b*.)

Male.

	A.	B. *teneral.*	C.	D.	E.	F.	G.	H.	I. *senegallus.*
C. I.	·76	·77	·78	·76	·77	·78	·76	·78	·80
l.	1·6	1·43	1·62	1·59	1·58	1·67	1·51	1·58	1·62
b.	·41	·40	·42	·41	·44	·45	·43	·40	·42
b. t.	·31	·28	·32	·32	·32	·33	·32	·32	·33
b. h.	·32	·33	·34	·32	·33	·35	·32	·33	·33
l. h.	·42	·43	·43	·42	·43	·44	·42	·42	·42
G. A.	·34	—	·35	·34	·34	·34	·34	·34	·33
b. p.	·26	—	·27	·26	·26	·26	·27	·26	·25
P.	·08	—	·086	·081	·082	·081	·08	·081	·8
p.	5 : 1	—	5 : 1	5 : 1	5 : 1	—	—	—	—
pen. l.	·035	—	·039	·037	·031	·035	·035	—	—
mesosome ...	·086	·093	·094	·089	·09	·093	·089	·089	·09

Text-figure 4.



Male genitalia of (a) *Syrrhaptœcus mitratus* Waterst. (b) *Syrrhaptœcus uncinosus* Waterst.

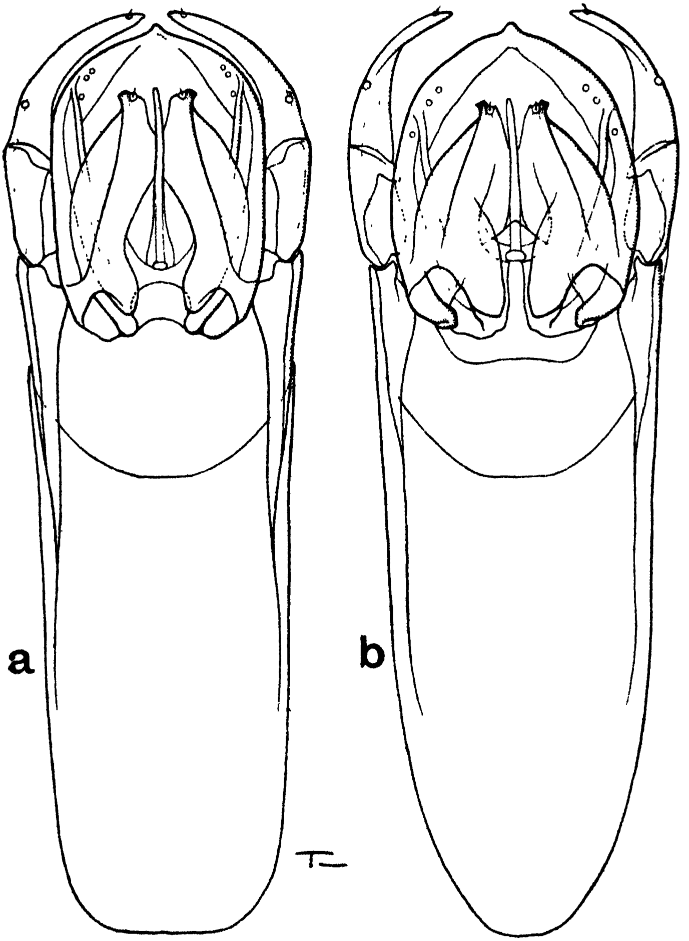
Female.

	A.	B.
C.I.	·77	·76
l.	2·37	2·14
b.	·58	·51
b. t.	·48	·36
b. h..........	·42	·38
l. h.	·54	·60

Chætotaxy normal.

Host, ***Pterocles senegalensis*** **Licht. and var.** ***orientalis*** **Hasselq.**

Text-figure 5.



Male genitalia of (a) *Syrrhaptœcus pallasi* Waterst. (b) *Syrrhaptœcus declivis* Waterst.

2 ♂, India, Wadali, Ahmednugger, 16. xi. 1876 (Dr. S. B. Fairbank Coll.). ♂, N. India, 10. x. 1886 (Warwick Coll.). Also the following localities (Africa):—2 ♂, 2 ♀, larva, **Holotype, Allotype,** and **Paratypes,** Sudan, Khartoum, Kerreri, 3. xii. 1909 (A. L. Butler Coll.). ♂, Sudan, Shendi, 3. iii. 1901 (Rothschild & Wollaston Coll.). 2 ♂, Lake Rudolf, 7. iv. 1900 (J. J. Harrison Coll.). Straggler from *Pterocles senegallus* Linn., ♂, Sudan, Red Sea Province, Erkowit, 8. iv. 1914 (Chapman & Lynes Coll.).

SYRRHAPTŒCUS sp.

Host, *Pterocles senegallus* Linn.

♂, India, Mehur, 18. i. 1872 (Hume Coll.). One of the "*mitratus*" group, and therefore probably a straggler on this host. In any case, too damaged for determination.

SYRRHAPTŒCUS DECLIVIS, sp. n. (Text-figs. 5 *b*, 9 *e*.)

Male.

	A.	B.
C. I.	·77	·77
l.	1·9	1·76
b.	·54	·44
b. t.	·37	·34
b. h.	·37	·35
l. h.	·48	·46
G. A.	·40	·38
b. p.	·29	·27
P.	·11	·11
p.	6 : 1	6 : 1
pen. l.	·065	·064
mesosome.	·139	·135

Female.

	A.	B.	C.	D.
C. I.	·76	·76	·74	·79
l.	2·77	2·29	2·18	2·28
b.	·72	·54	·53	·52
b. t.	·48	·40	·38	·48
b. h.	·45	·41	·39	·44
l. h.	·59	·54	·53	·55

Abdominal chætotaxy normal.

Valve 12, 12.

Host, *Eremialector bicinctus* Temm.

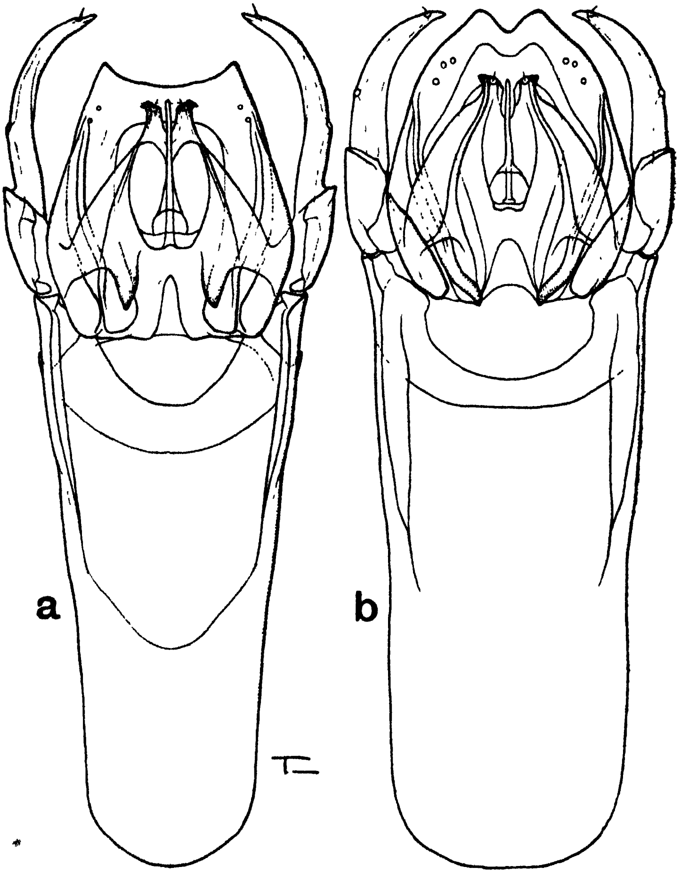
2 ♂, 4 ♀, **Holotype**, **Allotype**, and **Paratypes**, S. Africa, Angola, Benguella, Huxe, 30. viii. 1905 (Dr. J. W. Ansorge Coll.).

SYRRHAPTŒCUS MITRATUS, sp. n. (Text-figs. 4 *a*, 9 *a*.)

Male.

	A.	B.	C.	D.
C. I.	·79	·79	·81	·81
l.	1·6	1·57	1·55	1·59
b.	·47	·45	·48	·45
b. t.	·32	·32	·32	·31
b. h.	·35	·35	·35	·35
l. h.	·44	·44	·43	·43
G. A.	·36	·37	Not dissected.	·37
b. p.	·24	·26	"	·23
P.	·128	·13	"	·128
p.	6 : 1	6 : 1	"	6½ : 1
pen. l.	·072	—	—	·077
mesosome.	·14	·14	·14	·14

Text-figure 6.



Male genitalia of (a) *Syrrhaptœcus angulatus* Waterst. (b) *Syrrhaptœcus excisus* Waterst.

Female.

	A.	B.	C.
C. I.	·845	·86	·84
l.	2·11	2·08	2·00
b.	·60	·55	·57
b. t.	·39	·38	·39
b. h.	·43	·42	·41
l. h.	·51	·49	·49

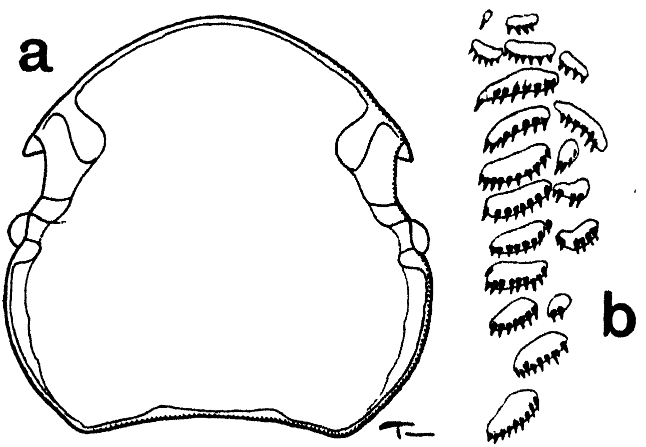
Abdominal chætotaxy normal.

Valve 10–11, 5.

Host, *Eremialector coronatus* Licht.

3 ♂ & larva, **Holotype** and **Paratypes**, Muscat (Mills Coll.). From India the following:—♂, ♀, **Allotype**, Kashgar (Dr. Bellew—Indian Museum). ♀, Sindh, Erie Hills, 1.xii. 1874 (Hume Coll.). ♀, larva, Upper Sind, Shikaipur, 15.iii. 1875 (W. T. Blanford Coll.).

Text-figure 7.



Syrrhaptœcus brevifrons Waterst. Female. (*a*) head; (*b*) crop teeth.

SYRRHAPTŒCUS sp.

Female.—C. I., ·76; l., 2·07; b., ·54; b. t., ·38; b. h., ·38; l. h., ·50.

Chætotaxy normal.

Host, *Eremialector decoratus* Cab.

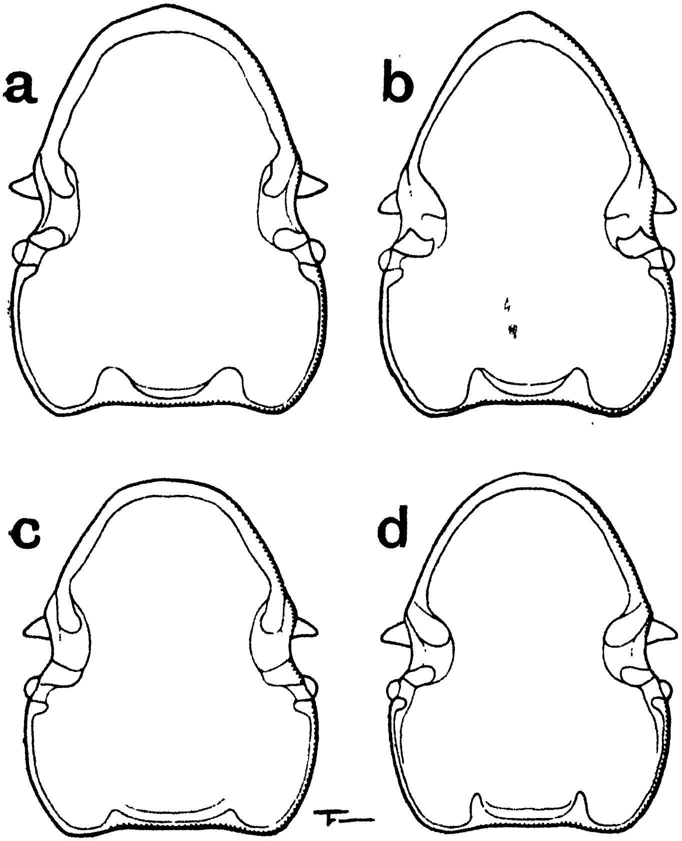
♀, Africa, below Lake Lambo, N'Guaso Nyno, 7.iii.1912 (Col. Stephenson Clarke Coll.).

This example is so close to *S. digonus* and *S. falcatus* that, in the absence of a male. its further determination cannot be attempted. It shares with the species referred to the narrow opening of the head of the pleurite.

SYRRHAPTŒCUS UNCINOSUS, sp. n. (Text-figs. 4 *b*, 8 *d*, 10 *a*.)

Male.—C. I., ·80; l., 1·7; b., ·5; b. t., ·34; b. h., ·37; l. h., ·46; G. A., ·42; b. p., ·31; P., ·11; p., 7 : 1; pen. l., ·062; mesosome, ·14.

Text-figure 8.



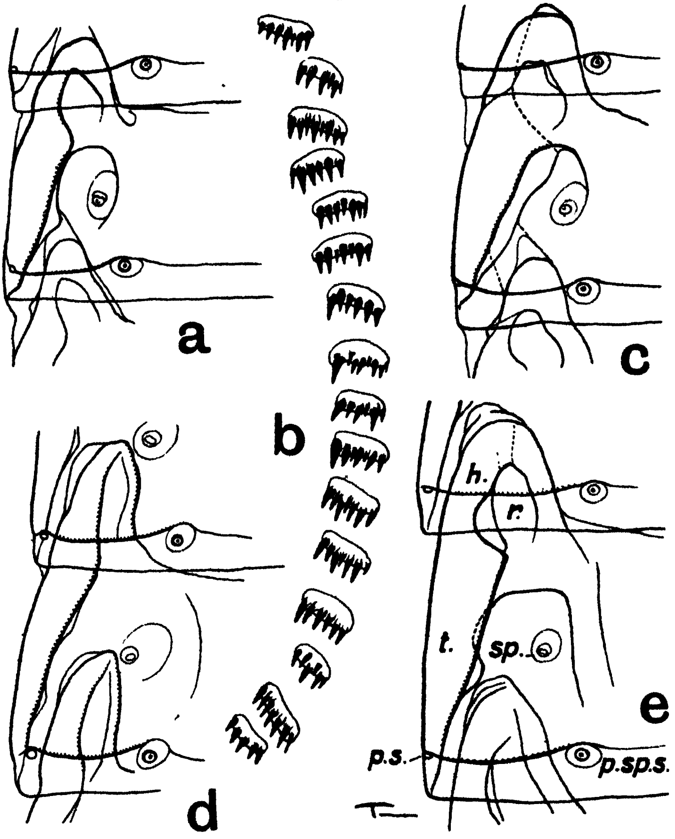
Outline of heads (female) of *Syrrhaptœcus* spp. (a) *S. angulatus* Waterst. (b) *S. digonus* Waterst. (c) *S. obtusus* Waterst. (d) *S. uncinosus* Waterst.

Female.

	A.	B.
C.I.	·81	·79
l.	2·02	1·94
b.	·54	·5
b. t.	·40	·35
b. h.	·42	·38
l. h.	·52	·48

Valve 10–11, 5.

Text-figure 9.



Details of *Syrrhaptœcus* spp. (female). (b) Crop teeth of *S. angulatus* Waterst. a, c, d, e, pleurites of 4th (5th) segment. (a) *S. mitratus* Waterst. (c) *S. bedfordi* Waterst. (d) *S. angulatus* Waterst. (e) *S. declivis* Waterst. In (e) *h.* "head" and *t.* "tail" of pleurite. *r.*, the ridge between the post spiracular bristle (*p.sp.s.*) and the lateral bristle (*p.s.*); *sp.*, spiracle.

Normal chætotaxy (abd.). *Female.*

	T.	Pl.	S.
I.	1, 1	0	—
II.	2, 2	0	1, 1
III.	1, 3, 3, 1	0	1, 1
IV.	1, 3, 3, 1	1	1, 1
V.	1, 3, 3, 1	1	1, 1
VI.	0, 3, 3, 0	2	1, 1
VII.	0, 3, 3, 0	2	2, 2 (1, 1)
VIII.	0, 3, 3, 0	4	1, 1
IX.	0	2/2	—

Host, *Eremialector gutturalis* Sm. and var. *saturatior* Hart.

♂, **Holotype**, Africa, T. T. Simba, 1915 (A. Loveridge Coll.). 2 ♀, **Allotype** and **Paratypes**, S. Abyssinia, Lake Zwai, 20. xii. 1904 (P. C. Zaphiro—W. N. McMillan Coll.).

SYRRHAPTŒCUS ANGULATUS, sp. n. (Text-figs. 6 *a*, 8 *a*, 9 *b* & *d*.)

Male.

	A.	B.
C. I.	·72	·75
l.	1·93	1·9
b.	·46	·44
b. t.	·36	·35
b. h. ...	·36	·36
l. h.	·50	·48
G. A.	·38	·37
b. p.	·26	·26
P.	·12	·12
p.	10 . 1	9-10 : 1
pen. l. . . .	.067	·0675
mesosome ...	—	—

Female.

	A.	B.
C. I.	·79	·79
l.	2·36	2·37
b.	·55	·55
b. t.	·42	·44
b. h.	·41	·435
l. h. . ..	·52	·55

Abdominal chætotaxy normal.

Valve 12, 6.

Host, *Eremialector indicus* Gmel.

2 ♂, **Holotype** and **Paratype**, India, Gurgaon Dist., 4. i. 1868 (Hume Coll.). ♀, **Allotype**, India, Gambhur, 2. vi. 1873 (R. M. Adam—Hume Coll.). ♀, N.W. India (Capt. Pinwill Coll.).

SYRRHAPTŒCUS PALLASI, sp. n. (Text-fig. 5 *a*.)

Male.

	A.	B.	C.	D.
C. I.	·77	·78	·78	·76
l.	1·5	1·55	1·56	1·49
b.	·44	·44	·47	·46
b. t.	·31	·3	·31	·30
b. h.	·34	·35	·35	·33
l. h.	·44	·45	·45	·44
G. A.	·34	·36	—	—
b. p.	·26	·27	—	—
P.	·08	·086	—	—
p.	5 : 1	5½ : 1	—	—
pen. l.	·065	·063	—	—
Mesosome ...	·10	·109	·109	·11

Host, *Eremialector orientalis* Linn.

4 ♂, **Holotype** and **Paratypes**, India, Punjab, nr. Fazilka, 15. xi. 1867 (Hume Coll.).

SYRRHAPTŒCUS OBTUSUS, sp. n. (Text-fig. 8 *c*.)

Female (not ovigerous).—C. I., ·85 ; l., 1·84 ; b., ·54 ; b. t., ·40 ; b. h., ·40 ; l. h., ·47.

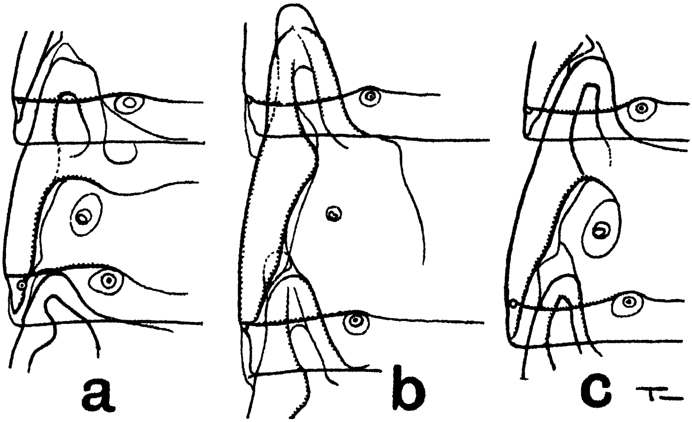
Chætotaxy normal.

Valve 10, 4.

Host, *Eremialector personatus* Gould.

♀, **Holotype**, Madagascar.

Text-figure 10.



Pleurites of 4th (5th) segment *Syrrhaptœcus* spp. (a) *S. uncinosus* Waterst. (b) *S. falcatus* Waterst. (c) *S. digonus* Waterst.

SYRRHAPTŒCUS EXCISUS, sp. n. (Text-fig. 6 *b*.)

Male (2).—C. I., ·73 ; l., 1·86 ; b., ·46 ; b. t., ·36 ; b. h., ·34 ; l. h., ·47 ; G. A., ·42 ; b. p., ·30 ; P., ·12 ; p., 7 : 1 ; pen. l., ·057 ; mesosome, ·12.

Host, *Eremialector quadricinctus* Temm., var. *lowei* C. Grant.

♂ **Holotype** and ♂ **Paratype**, Sudan, Kordofan, El Obeid (N. G. B. Halked Coll.). (Found on two separate birds.)

Key to the Species of Syrrhaptœcus.

1.	Forehead (♂, ♀) shorter than hind head; C. I. over I.; tergites IV.-V. with bristles 1, 4, 4, 1	*brevifrons* Waterst.
	Fore and hind head subequal; C. I. at most slightly over ·9	2.
2.	Males	3.
	Females	13.
3.	Third joint of antenna distally expanded or with appendix.	4.
	Third joint of antenna simple	5.

4. Third joint widened distally and projecting there anteriorly; abdomen very bristly, tergites IV.–V. with bristles 1, 8, 8, 1; head broad, C. I. ·88–·89; mesosome broader than long .... *tibetanus* Waterst.

   Third joint apically with short recurved appendix; tergites IV.–V. with bristles 1, 2, 2, 1; head narrower, C. I. ·84–·85; mesosome ogival, longer than broad .... *alchatæ* Rudow.

5. Mesosome mitre-shaped (*i. e.* parabolic with a short median apical tooth) (text-figs. 4, 5) .... 6.

   Mesosome variable (apically truncate, bidentate, emarginate, etc.) .... 9.

6. Basal plate short and distally broad; mesosome large, over half as long as the basal plate .... *mitratus* Waterst.

   Basal plate narrower; mesosome relatively much shorter. 7.

7. Telomers strongly reflexed; paramers narrow (7 : 1) .... *uncinosus* Waterst.

   Telomers less prominent; paramers broader (6 : 1 or less). 8.

8. Mesosome evenly curved from apex to base of paramers . *declivis* Waterst.

   Mesosome parallel-sided for about two-thirds from base . *pallasi* Waterst.

9. Mesosome notably broad; apical edge simple; upper and lower plates of nearly equal length; paramer short, sickle-shaped .... *falcatus* Waterst.

   Mesosome longer than broad, and otherwise without the above combination of characters .... 10.

10. Paramers slender, basally thicker and flattened mainly towards apex, basal collar prominent; mesosome with sides nearly straight, the apex broadly and deeply concave .... *angulatus* Waterst.

    Paramers flat throughout their whole length, the basal collar not prominent .... 11.

11. Mesosome parabolic, deeply and rectangularly emarginate at apex .... *excisus* Waterst.

    Mesosome more broadly curved, at most subconcave apically .... 12.

12. Paramers sickle-shaped; apex of mesosome slightly concave in middle, the angles at sides of the concavity not produced; telomers blunt; head broad, C. I. ·84–·86 *bedfordi* Waterst.

    Paramers inflexed on apical third; mesosome broadly truncate at apex, with prominent lateral angles; telomers angulate, reflexed; head narrower, C. I. ·77–·80. *digonus* Waterst.

13. Head broad, C. I. ·90–·91; chætotaxy not normal .... 14.

    Head narrower, C. I. not exceeding ·87; chætotaxy normal. 15.

14. Chætotaxy: T. IV.–T. V., 1, 8, 8, 1; tail of pleurite very broad and longer than head .... *tibetanus* Waterst.

    Chætotaxy: T. IV.–T. V., 1, 2, 2, 1; tail of pleurite not unusually thick and not longer than head .... *alchatæ* Rudow.

15. Head: C. I., ·83–·87 .... 16.

    Head: C. I., ·81 or less .... 18.

16. Head subtruncate (text-fig. 8 *c*) .... *obtusus* Waterst.

    Head evenly parabolic .... 17.

17. Pleurites expanding more rapidly towards the head (text-fig. 9 *c*) .... *bedfordi* Waterst.

    Pleurites more parallel-sided (text-fig. 9 *a*) .... *mitratus* Waterst.

18. Forehead sub-ogival, strongly contracted before the antennæ; enclosed space in heads of pleurites narrow . *digonus* Waterst.

    Forehead more parabolic anteriorly or even subtruncate . 19.

19. Forehead evenly parabolic .... 20.

    Forehead anteriorly subtruncate .... 21.

20. Hind head at widest not extending beyond the tips of the trabeculæ; head of pleurites large and subtriangular, the enclosed space wide (text-fig. 10 *a*) ... . *uncinosus* Waterst.
Hind head wider; heads of pleurites with their enclosed spaces narrower (text-fig. 10 *b*) .... *falcatus* Waterst.

21. Pleurites strongly developed; head reaching anteriorly to level of the spiracle; inner, ventral, and lateral angulation of the "tail" slight (text-fig. 9 *d*).. .... *angulatus* Waterst.
Pleurites shorter and broader, not reaching the spiracle; lateral angle of tail distinct (text-fig. 9 *e*) .... *declivis* Waterst.

NEOMENOPON PTEROCLURUS Bedf.

Neomenopon pterocłurus Bedford, G. A. H., Parasitology, xii. no. 2, pp. 170–172, pl. xiii. figs. 1, 2 (13. iii. 1920).

Host, *Pterocles alchata* Linn.

4 larvæ, Palestine, Gaza, 20. viii. 1917 (Maj. A. G. L. Sladen Coll.).

I have to thank Mr. Bedford for the privilege of examining the type of *N. pterocłurus*, which was originally found on *P. namaquus* Gm. (S. Africa, Transvaal, Rustenburg Dist.). This interesting Menoponid species doubtless occurs on every species of Sand-Grouse.

SUMMARY.

1. Skins of the 16 known species of Pteroclidæ have been examined in the British Museum, and 14 species of Mallophaga referable to two genera, both peculiar to Sand-Grouse, have been collected from 14 host species.
2. The methods of collecting and preparation are described.
3. A list of hosts and parasites is given.
4. Judged by their parasites, Sand-Grouse are related to the grouse and pheasants.
5. Descriptions of a new genus and twelve new species are given, and a key appended.

18. The Species of *Notogonia* (Hymenoptera, Larridæ), occurring in the Mediterranean Basin. By O. W. Richards, M.A.*

[Received April 3, 1928: Read May 1, 1928.]

The difficulty I experienced in identifying a species of *Notogonia* captured in the South of France in August 1927 has led me to hope that a summary of the differences between the Mediterranean species might prove useful. My thanks are due to Prof. E. B. Poulton for permission to study the Morice collection at Oxford, to Dr. J. Waterston for much kind help in the examination of the material in the British Museum, and to Dr. F. Maidl, who lent me specimens of certain species from the Viennese Museum. The arrangement of the species of this genus in the British Museum collection is due to Mr. R. E. Turner, and much of the synonymy here published is really based on his work.

Key to the Females.

1 (4). Pygidial area shining, only punctured at all closely towards its apex, not covered with closely-set decumbent pubescence. Clypeus with a fairly wide, smooth, unpunctured apical area, which is produced upwards as a slight central keel. (Mesonotum and mesopleura not punctured, but very finely rugulose.)

2 (3). Pygidial area narrower, quite closely and finely punctured at the apex. Median segment with its dorsal area finely wrinkled, with transverse striæ indicated; its sides and posterior surface regularly striate .... *pompiliformis* Pz.

3 (2). Pygidial area broader, the punctures larger and not fine and close at the apex. Median segment with the sculpture much more obsolete; striæ faintly indicated only on the upper half of the sides of the median segment and on the lateral part of its posterior surface .... *opalipennis* Kohl.

4 (1). Pygidial area dull, closely punctured, except at the extreme base, which, however, is usually hidden by the preceding tergite, covered with dense, silvery, decumbent pubescence. Clypeus with a narrower, unpunctured apical area.

5 (12). Mesonotum and mesopleura finely rugulose, dull. Median segment with its dorsal area finely wrinkled. (Size large; sides of median segment either with very fine, very close striæ, or, if more strongly striate, the striæ are more or less interrupted in the posterior part.)

6 (9). Sides of the median segment with coarse striæ widely interrupted on the disc, especially posteriorly. (Wings not very dark. Posterior surface of the median segment regularly striate at its sides, smoother on its disc.)

---

* Communicated by the Secretary.

7 (8). Striæ of sides of median segment more effaced posteriorly. Hind femora black .... *memnonia* Smith.

8 (7). Striæ of median segment stronger. Hind femora red .... *subtessellata* Smith.

9 (6). Sides of median segment with no coarse striæ. (Hind femora black.)

10 (11). Sides of median segment practically smooth. (Species very much resembling *N. memnonia* Sm.) *trivittata* Kirby.

11 (10). Sides of median segment with very fine, very closely set, fairly regular striæ (very different from those of any of the other species). Dorsal surface of the median segment posteriorly defined by a strong keel; some very strong longitudinal keels on the part where the lateral and posterior surfaces join; striæ on the disc of the posterior surface irregular. (Wings dark, with a metallic blue reflection.). . *nigrita* Lep.

12 (5). Mesonotum and mesopleura (especially the epimera) shining, obviously punctured (except the epimera). Dorsal area of the median segment very coarsely wrinkled.

13 (14). Upper part of mesopectus strongly and fairly densely punctured .... *prætermissa*, sp. n.

14 (13). Upper part of the mesopectus much less strongly and densely punctured . ... *nigricans* Walker.

Key to the Males.

The sculpture of the thorax and median segment of the males usually resembles that of their respective females, but is often less strong.

1 (6). Hind femora beneath either longitudinally furrowed or excavated near the base, leaving an angle projecting. (Antennæ as in *N. pompiliformis.*)

2 (3). Hind femora beneath longitudinally excavate, so that the postero- and antero-ventral edges are raised into keels. (Wings rather dark. Decumbent hairs on sternites 5–7 longer than those on the previous sternites; 7th with a ridge of short outstanding hairs on each side; 8th slightly emarginate.) .... *nigrita* Lep.

3 (2). Hind femora excavated beneath so as to leave a projecting angle near the base.

4 (5). Hind femora more strongly excavate. Front and mid femora nearly bare. 4th sternite widely emarginate; 5th widely emarginate, with a long tuft of hairs on each side; 8th slightly emarginate. *memnonia* Smith.

5 (4). Hind femora less strongly excavate. Front and mid femora with a dense fringe of white hairs. 6th sternite broadly emarginate; 7th with a ridge of hairs on each side; 8th slightly emarginate ...... *trivittata* Kirby.

6 (1). Hind femora simple.

7 (10). Mesonotum and mesopleura dull, finely rugulose, not punctured. None of the apical sternites with outstanding hairs; 8th sternite slightly emarginate.

8 (9). Hind femora red. Sides of median segment with the striæ partly effaced posteriorly, though not so much as in the female. (Antennæ as in *N. pompiliformis.*) .... *subtessellata* Smith.

9 (8). Hind femora black. Sides of the median segment with the striæ stronger and more regular. Antennæ with the 3rd joint much longer than the 2nd, joints 3–13 all distinctly elongate (more than twice as long as broad) and subequal . ... *pompiliformis* Pz.

10 (7). Mesonotum finely punctured, not very dull; mesopleura, especially the epimera, shining Some of the apical sternites with dense outstanding hairs; hairs of the 7th and 8th sternites much shorter; 8th sternite not emarginate.

11 (12). The upper part of the mesopectus quite strongly and closely punctured. Antennæ as in *N. pompiliformis*. Apex of the 3rd and 4th sternites and whole of the 5th with rather long outstanding hairs .. .. *prætermissa*, sp. n.

12 (11). Upper part of the mesopectus more finely and sparsely punctured. Antennæ with the 2nd joint very short; 3–5 each a little longer than the 2nd; 6th joint about one and a half times as long as the 5th; 6–13 subequal, distinctly elongate (more than twice as long as broad). Apex of the 4th sternite and whole of the 5th and 6th with rather long outstanding hairs .. .. *nigricans* Walker.

I have not been able to examine a male of *N. opalipennis* Kohl.

Notes on the Species.

1. Notogonia pompiliformis Pz.

Larra pompiliformis Panzer (1809, p. 106).
Larrada agilis Smith (1856, p. 284).
Tachytes nigra Fabre (1886, p. 230).
Larra nigriventris Cameron (1889, p. 127).
Larra nana Bingham (1897, p. 200).
Larra iridipennis Cameron (1900, p. 26).

The types of the species given in the synonomy, except Fabre's species, are all in the British Museum. All are females, and, so far as can be judged in this sex, do not differ essentially from European *pompiliformis*, though in the Indian examples there is a tendency for the striæ of the lateral surfaces of the median segment to be partially effaced. The African examples (= *agilis* Sm.; also a female from St. Vincent, Cape Verde Islands) also appear to be *pompiliformis*.

The species is widespread in the Mediterranean region, where it would appear to be the commonest species of its genus. Adults emerge from their cocoons in the late summer and soon take to winter quarters; they are captured most commonly on their emergence in the spring. The nesting-habits have been described by Kohl (1894, p. 252), Fabre (1886, p. 230), Ferton (1901, p. 98; 1905, p. 67; 1910, p. 152; 1911, p. 359), and Berland (1925, p. 43). The female hunts crickets, *Platyblemmus umbroculatus* Luc., *Gryllomorpha dalmatina* Ocsks., and *G. uclensis* Pant. In the spring small specimens are captured, late in the year almost full-grown larvæ, in either case the prey being very imperfectly paralysed. In the larger prey one or more of the legs is bitten off to impede movement. The egg is laid transversely on the sternum between the fore and mid pairs of legs. The nest is a shallow tunnel in the earth, only 5–6 cms. deep, leading to a few cells (1–3) situated at the end of short branch tunnels. Berland found the Tachinid fly, *Sphecapata conica* Fall., as a parasite.

2. NOTOGONIA OPALIPENNIS Kohl (1898, p. 98).

This species was described from Oran and Biskra. I have seen a female (Oran), determined by Kohl, kindly lent me by Dr. F. Maidl. The character of the pygidial area and of the median segment appear to be sufficiently diagnostic, but one would like to see a long series, including some males.

3. NOTOGONIA SUBTESSELLATA Smith (1856, p. 277).

This is mainly an Oriental species, but two females and one male from Amara, Mesopotamia, are in the Morice collection. The habits have been observed by G. R. Dutt (1912, p. 198; also in Lefroy, 1909, p. 201). It preys on immature crickets of the genus *Gryllodes*. These are dug out of the ground, the wasp never penetrating the cricket's own burrow, even when it is available. Crickets often make good their escape by jumping, and the wasp is only successful after several attempts. When captured the prey is given one or two stings at the junction of the pro- and mesosternum. The cricket is gripped by the antenna, the wasp straddling over it and walking forwards till it climbs up some plant to a foot or so above the ground and flies laboriously away. In approaching the actual nest, the wasp walks backwards, dragging the prey after her. Probably the burrow is made before the prey is captured; the hollow stem of some plant may be used as a burrow, or it may be dug in the soil.

4. NOTOGONIA NIGRITA Lep.

Tachytes nigrita Lepeletier de St. Fargeau (1845, p. 211).
Notogonia pharaonum Kohl (1907, p. 220).

Though the kindness of Dr. F. Maidl, I have examined the unique type of *N. pharaonum* Kohl, which was captured in Egypt; it appears to me to be only a rather small male of *N. nigrita*. This species is, after *N. pompiliformis*, the commonest if its genus in the Mediterranean region. Captures appear to be most frequent between March and May, but there are three females in the Morice collection taken by Donisthorpe at Bordighera on the 31st of January. Ferton (1911, p. 359) has made some observations on its habits, at La Calle in Algeria. It was found hunting larval crickets in late August and September, looking for them under stones. The wasp was often unsuccessful in its attempts at capture. The burrow is fairly deep, and is often made in the sides of some natural cavity, such as the hole of a rodent. Saunders (1911, p. 97) also records Eaton's observation of *N. nigrita* preying on a cricket at Biskra on the 22nd of March, so that there are two periods of the year for hunting.

5. NOTOGONIA MEMNONIA Sm.

Larrada memnonia Smith (1856, p. 281).
Larrada subfasciata Walker (1871, p. 21).
Notogonia argyropyga Costa (1878, p. 17, footnote).

The types of Smith's and Walker's species, both unique females, are in the British Museum. They appear to be identical with the species better known as *N. argyropyga* Costa. This has an eastern and southern distribution; I have seen specimens from Egypt and Mesopotamia.

6. NOTOGONIA TRIVITTATA Kirby.

Tachytes trivittatus Kirby (1900, p. 16).
Larra (Notogonia) expedita Kohl (1907, p. 219).

Kirby's type is a female in the British Museum, where also is one of the co-types of Kohl's species. All the specimens I have seen came from Sokotra.

7. NOTOGONIA PRÆTERMISSA, sp. n.

For reasons given in the notes on the next species, I think the present form requires a new name. The type series is five females and one male captured in Ile de Porquerolles, Var, France, in August 1927. The actual type is a male in the collection of the British Museum captured on the 26th of August. The species was not uncommon at damp spots on the cliffs of the island, where also *Pseudagenia carbonaria* Scop., to which the *Notogonia* bears a striking resemblance, was even more common. I have also seen specimens from Corfu; Barcelona; Alger; Tunis; Biskra; Resht, Persia; Mersina, Anatolia; Siala, Soudan.

Description.

Black, with short silvery hairs, especially visible on the clypeus, apices of the 1st to 3rd abdominal tergites, and on the pygidium. Wings slightly infuscate, more so in the female. Head and abdomen smooth; thorax with fine and close punctures, which are coarsest on the episterna and almost absent from the epimera. Median segment rather coarsely rugose, becoming irregularly striate on the sides and on the posterior surface. Pygidial area of the female entirely dull and covered with short silvery hairs. Abdomen of the male with the apex of the 3rd and 4th sternites and the whole of the 5th with distinct outstanding dark hairs; hairs of the 6th and 7th much shorter; 8th not emarginate. Eyes in the male separated by as much as the length of the 2nd and 3rd antennal joints, in the female by not quite so much. Antennæ in both sexes with the 3rd joint rather more than twice as long as the 2nd, the joints from the 3rd onwards subequal and rather more than twice as long as broad. Claws simple. Length: male 6–8, female 8–12 mm.

8. NOTOGONIA NIGRICANS Walker.

Larrada nigricans Walker (1871, p. 21).
Notogonia sculpturata Kohl (1892, p. 221).
Larra (*Notogonia*) *palumbula* Kohl (1894, p. 304).
Leptolarra reticulata Cameron (1900, p. 31).
Notogonia nigricans Turner (1917, p. 319).

A female co-type of Walker's species is in the British Museum. The type of *sculpturata* Kohl was a male from Egypt. Dr. Maidl sent material from Vienna that included the type, though the latter was not specifically indicated. In this series two males from Egypt both belonged to *nigricans*, while a male and female from Barcelona belonged to the species just described as *prætermissa*. The type of *palumbula* Kohl is probably in the collection of Dr. Brauns, of Willowmore, and was not available for study, but I have seen a specimen from Sokotra determined by Kohl.

Cameron's type was also not available, but I follow Mr. R. E. Turner (1917, p. 319), who states that it is an Indian subspecies with a rather more finely punctured mesonotum. Examination of a considerable number of specimens has left me unable to distinguish in any way between the South and East African *palumbula* Kohl and the Egyptian and Arabian form, *N. nigricans* Walk. I have seen specimens of this species from Cairo and Fayum; Djama, S. Algeria; Amara, Mesopotamia; Aden; various localities in E. and S. Africa, *e. g.* N.E. Rhodesia, Cape Province; Gibraltar; females of apparently the same species from St. Vincent, Cape Verde Islands.

It is unfortunate that in all collections females so predominate; some of the forms here treated as one species may prove to be distinct when the males are known.

BIBLIOGRAPHY.

BERLAND, L. 1925. Notes sur les Hyménoptères fouisseurs de France. VI. Observations Biologiques. Ann. Soc. Ent. France, xciv. pp. 39–51.

BINGHAM, C. T. 1897. The Fauna of British India. Hymenoptera, vol. i. London.

CAMERON, P. 1889. Hymenoptera Orientalis, part i. Mem. Manchester Lit. & Philos. Soc. (4) ii. pp. 91–152.

—— 1900. Descriptions of New Genera and Species of Aculeate Hymenoptera from the Oriental zoological region. Ann. Mag. Nat. Hist. v. (7) pp. 17–40.

COSTA, A. 1878. Relazione di un Viaggio per l'egitto, &c. Atti Acad. Sc. Fis. Napoli, vii. no. 2, pp. 1–40.

DUTT, G. P. 1912. Life-histories of Indian Insects. IV. Hymenoptera. Mem. Dept. Agric. Ent. Ser. India, iv. pp. 183–267, 20 figs., pls. xi.–xiv.

FABRE, J. H. 1886. Souvenirs Entomologiques, 3me sér. Paris.

Ferton, C. 1901. Notes détachées sur l'instinct des Hyménoptères mellifères et ravisseurs. Ann. Soc. Ent. France, lxx. pp. 83–148, pls. i.–iii.

—— 1905. Notes détachées, 3me ser. Ann. Soc. Ent. France, lxxiv. pp. 56–104, pls. iii.–iv.

—— 1910. Notes détachées, 6me sér. Ann. Soc. Ent. France, lxxix. pp. 145–178.

—— 1911. Notes détachées, 7me sér. Ann. Soc. Ent. France, lxxx. pp. 351–412.

Kirby, F. 1900. The Expedition to Sokotra. Description of New Hymenoptera. Bull. Liverpool Mus. iii. pp. 13–24.

Kohl, F. F. 1884. Die Gattungen und Arten der Larriden. Verh. Zool.-Bot. Ges. Wien, xxxiv. pp. 171–268, pls. vii.–viii.

—— 1892. Neue Hymenopteren. Ann. k.-k. Naturhist. Hofmus. Wien, vii. pp. 197–232, pls. xiii.–xxiv.

—— 1894. Zur Hymenopterenfauna Afrikas. Ann. k.-k. Naturhist. Hofmus. Wien, ix. pp. 279–350, pls. xiii.–xvii.

—— 1898. Neue Hymenopterenformen. Ann. k.-k. Naturhist. Hofmus. Wien, xiii. pp. 91–102.

—— 1907. Zoologische Ergbnisse der Expedition der Kaiserlichen Akademie der Wissenschaft nach Süd Arabien und Sokotra im Jahre 1898–9. Hymenopteren. Denskr. K. Akad. Wiss. Wien, lxxi. pp. 169–301, pls. i.–xi.

Lefroy, H. M. 1909. Indian Insect-Life. Calcutta.

Lepeletier de St. Fargeau, A., et **Brullé**. A. 1845. Histoire Naturelle des Insectes. Hyménoptères, iii. Paris.

Panzer, G. W. F. 1809. Faunæ Insectorum Germanicæ initia oder Deutschlands Insecten, ix. Nürnberg.

Saunders, E. 1911. Hymenoptera Aculeata collected in Algeria. The Sphegidæ. Trans Ent. Soc. Lond. pp. 62–135.

Smith, F. 1856. Catalogue of the Hymenopterous Insects in the Collection of the British Museum. Part iv. London.

Turner, R. E. 1917. Notes on the Fossorial Hymenoptera. XXVI. On New Species in the British Museum. Ann. Mag. Nat. Hist. (8) xix. pp. 317–326.

19. The Morphology of the Cicadidæ (Homoptera). By J. G MYERS, Sc.D.*, Imperial Bureau of Entomology, late 1851 Science Exhibition Scholar.

[Received March 20, 1928: Read April 17, 1928.]

(Text-figures 1–75.)

CONTENTS.

	Page
Introduction	365
(1) External Anatomy	365
a. General Characters	365
b. Integument and Coloration	366
c. Head and its Appendages	368
d. Thorax and its Appendages	380
e. Abdomen and its Appendages	402
(2) Internal Anatomy	413
a. Nervous System and Sense-Organs	414
b. Muscular System	426
c. Respiratory System	426
d. Alimentary System	433
e. Circulatory System	456
f. Fat-Body	456
g. Reproductive System	456
(3) Sound-Organs	459
a. Description of Sound-Organs	460
b. Historical Review	467
c. Accessory stridulating apparatus of Tettigadinæ	472

INTRODUCTION.

In spite of their size and the interest which their loud song has excited in Man from the earliest times, the Cicadas have been extraordinarily neglected by morphologists. The sound-producing apparatus has been the subject of considerable study and much controversy, but the rest of their structure has remained almost unknown or greatly misunderstood. The following study was made largely in the Entomological Laboratory of the Bussey Institution, Harvard University, and I am deeply indebted to Professor W. M. Wheeler and to Professor C. T. Brues for help and advice of every kind during its course.

(1) EXTERNAL ANATOMY.

a. GENERAL CHARACTERS.

The Cicadas are among the largest insects included not only in the Homoptera but in the whole Order. Their shape, with the body usually short and stout and the wings long or moderately so, is rendered characteristic by the normally short but wide head, with prominent eyes and conspicuous ocelli, frequently red in colour, and arranged in a triangle upon the crown. The head may be produced, but never to such an extent as in the Fulgoridæ—the only other Homoptera nearly rivalling the larger cicadas in size.

---

* Communicated by S. A. NEAVE, M.A., D.Sc., F.Z.S.

The fore-legs show great swollen spinose femora, while the wings, though strong, are usually transparent, but in some cases opaque and highly coloured. The venation is comparatively primitive and simple, with, in addition, an ambient vein cutting off a fairly wide border.

The males of all save one genus possess a complicated sound-producing organ in the 1st abdominal segment, while both sexes are furnished with the most complex chordotonal organ known, housed in a swelling on each side of the 2nd abdominal segment.

All the species are purely phytophagous, living on the sap of plants. The nymphs throughout the family are subterranean and noted for the extreme length of the cycle—in one well-established case reaching seventeen years. Their fore-legs are modified in a characteristic way for fossorial purposes.

The eggs are deposited in the stems of plants by means of the powerful ovipositor carried by the female. The young nymphs on hatching out drop at once to the ground and burrow.

The adults are comparatively short-lived, enduring at most one season. The song exhibits great constant specific variation and apparently plays a part in the mating preliminaries.

b. INTEGUMENT AND COLORATION.

The integument of cicadas is generally well-chitinized. The cuticle may be rarely entirely smooth or covered with pubescence or pilosity. The pubescence is often fine, close, and continuous, and may completely obscure the colour beneath. Silvery or gold markings formed by patches of pubescence are frequent. Pruinosity is less frequent than in Fulgoroidea or Sternorrhyncha. It is usually confined to the immediate neighbourhood—often a mere rim—of the more posterior abdominal spiracles, but may occur in patches elsewhere. Nevertheless, waxy material may exist as an extremely thin and practically imperceptible covering over the whole of the body-surface, as Fumouze (1888 *c*)* found in *Tibicen plebeia* and *Huechys sanguinea* by the use of chemical methods. Pilosity is associated chiefly with altitude. Among those New Zealand species of *Melampsalta* which enjoy a considerable range in altitudinal distribution, there is a clear correlation between elevation and hairiness. Alpine or subalpine species, however, are nearly always more hairy than closely-related lowland forms. *Tettigarcta crinita* Dist., perhaps the most profusely hairy of known cicadas, occurs on Mt. Kosciusko at an elevation of 5000 feet (H. Ashton, *in litt.*).

The colour-pattern of Cicadas contains usually two elements—an arrangement of dark cuticular markings on a paler hypodermal ground-colour. Sometimes one will predominate; sometimes the other.

Metallic colours would seem to be absent, but are occasionally simulated by pubescence.

An interesting study of the pigmentation in *Magicicada septendecim* has been made by Gortner (1911)*. He remarks that the rapid change from the pale-coloured, almost creamy, nymph to the deep black adult "presents one of the most remarkable changes in coloration" of which he is aware. From his earlier work on the pigmentation of the meal-worm (*Tenebrio molitor*) he had expected to find that this change in colour was an oxidation, induced by the action of an oxidizing enzyme, and his expectation was fully realized, although he found important differences.

The colour "is due to the action of a tyrosinase acting on some aromatic amino phenol, producing, as a result of the action, a black, insoluble pigment. That it is an oxidation is shown in the following ways" (Gortner, 1911):—

1. If an imago just emerged be placed in water no coloration appears; yet if it is removed at any time before decomposition sets in, the coloration proceeds at once.
2. If an imago just emerged be kept in a stream of CO_2 no colouring occurs; but if in O_2 the blackening proceeds normally.

There was no difference in the intensity or rapidity of coloration in insects kept during, and after ecdysis in strong light, dim light, total darkness, or light filtered through blue glass.

On p. 93 Gortner makes the interesting suggestion, inasmuch as the coloration is a uniform black over the entire surface,—

> "that the entire new cuticula is formed by the reaction between the oxidase and the chromogen, in the same manner that the Japanese lacquer is formed by the action of laccase on the milky latex of the tree *Rhus vernicifera*."

The wings are usually colourless, but in some cases opaque and brilliantly coloured. Grafin von Linden (1901) has studied the wing-markings, especially in some of the *Platypleura* spp., which show spots and streaks. She finds the markings are always determined in position either by the position of the veins themselves or of the minute cross-folds which may be seen in certain lights in every cicada tegmen and which she believes to be relics of a close net-veining. The strongest markings are determined in position by the few cross-veins which remain in the imago. Even in the most transparent tegmina there are frequently dark marks on the cross-veins or at the end-points of long veins. Biedermann (1914, pp. 1719–1721) discusses the Grafin's results.

---

* Full references are given in a comprehensive bibliography of the family now being published by Messrs. George Routledge & Sons, Ltd. in my book on the Biology of Cicadas.

It is unfortunate that the only two cicada species on which the chemists have worked were, from the pigmentation standpoint, highly anomalous. Fumouze studied the red medicinal Cicada, *Huechys sanguinea*, of the Orient. This species is coloured a striking red and black, and possesses in addition an unpleasant smell, and thus belongs to the forms commonly regarded as protected by "warning coloration." Fumouze (1888 *b*) isolated from it a red pigment—"rouge d'Huechys"—which gives the colour to the abdomen, and a yellow hygrometric substance.

c. HEAD AND ITS APPENDAGES.

The literature on the head and its appendages is almost entirely modern. After a few references in classical antiquity we find no more attention paid to this part of the cicada anatomy until comparatively recent times. The early post-Renaissance observers were interested chiefly in the sound-organs and worked but little on other parts of the cicada body.

Nevertheless, it would be a mistake to suppose that Aristotle missed anything which could be seen, if not exactly perceived, by the means at his command. He believed that cicadas lacked a mouth, or rather that the mouth and tongue were united so as to form a single part, through which, as through a root, the fluids on which they live are sucked up (de part. Animal. lib. iv. 5). We shall return to this conception when discussing feeding-habits. The Egyptians also saw the rostrum or "aculeus," and interpreted it as the plectrum of the musical instrument (Horapollo, Valeriano Bolzani). Pliny (lib. ii. cap. 37) quoted Nigidius to the effect that cicadas lack eyes—a statement which is repeated by Moufet (1634),—and is perhaps based on the lack of the wariness usual to cicadas and other insects in the common European species, *Tibicen plebeia*.

The modern references will not be discussed in detail until we have described the parts concerned. It will then be easier to correlate the results of previous work.

In later days some of the most controverted questions in external insect anatomy have concerned the interpretation of Hemipterous head-structure. Some member of the family Cicadidæ has very often been the type studied, as in the case of Smith with his startling homologies in 1892, Marlatt (1895), Meek (1903), and Muir and Kershaw (1911 *a*, 1911 *b*, 1912). Writers on other families of Homoptera have often orientated themselves on the large Cicadidæ; thus Funkhouser (1917) and Doering (1922). The literature is therefore bulky, but, in addition, the fact that Hemipterous head-structure is remarkably uniform throughout both suborders, brings in as explanatory of cicada conditions interpretations based on other forms, and adds to the list such classical contributions as those of Geise

(1883), Wedde (1885), and the more recent work of Bugnion and Popoff (1911), and Tower (1914). Thus it might reasonably be expected that the homologies of the trophi and sclerites have been clearly demonstrated. But this is very far from the case. Moreover, as at least two other contributions (Metcalf, Hussey) on the subject in America alone are now either in the press or in manuscript, the present writer feels that no finality for the interpretation here supported can be expected.

In a subject so much discussed it is, of course, obvious that the structures themselves have now become moderately well known and the discovery of strikingly new morphological evidence correspondingly unlikely. Until the homologies of the Hemipterous mouth have been finally elucidated by wider and more comparative embryological studies of this and of all related orders, coupled with an advance in our knowledge of insect morphology in general, with clearer conceptions of the relationships and origin of the head sclerites in the most primitive mandibulate forms, finality cannot be expected in the interpretation of cicada head-structure. In the following pages I have therefore, after an examination of all previously published views and a study of both nymphs and adult cicadas, chiefly of New Zealand species of *Melampsalta*, especially *M. cingulata* and *M. leptomera*, attempted first a simple description of the head and mouth-parts, and then a collation of the arguments for and against the various divergent views, the substantiation of which must lie *sub judice* at least until the publication of studies now in the press. For the adult condition, as Snodgrass has suggested, it is advantageous to study a soft freshly-emerged example, or even one extracted from the nymphal cuticle just before ecdysis.

Since the chief controversy concerns the homologies firstly of the two pairs of mouth-setæ and secondly of the facial sclerites, the description of these will be made especially detailed. Unless otherwise stated the particulars concern *Melampsalta leptomera* adult, of which a head cleaned by Nematode worms more neatly than by KOH was fortunately available.

a. Description of Head and Mouth-parts.

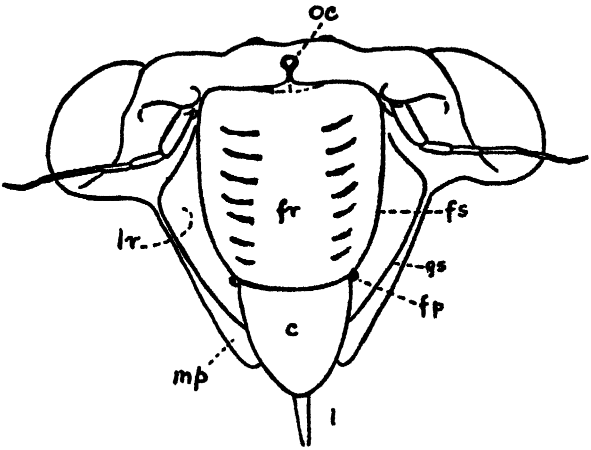
Viewed from the front, the most striking feature is the large, swollen, transversely-striated frons (text-fig. 1, *fr.*), of which the striations correspond with the insertions of the great dilator muscles of the sucking-pump. The upper edge of this sclerite passes into the crown or vertex*, from which it appears to be separated by a transverse fold rather than by a distinct suture. In the nymph at the final ecdysis the split does not occur along this fold but more caudally, along two sides of a wide triangle of which the fold in question forms the base. This triangular piece, which bears the median ocellus in the adult, is apparently rather a part of the true frons than of the true vertex. There seems no reason against considering the sides of the triangle as the arms of the epicranial suture (text-fig. 2, *es.*). There is a fairly distinct line along the arms of the Y in the adult head as viewed internally (text-fig. 2). The corresponding sclerite in Membracidæ, as shown by Hazel Branch *, may also be considered the frons. In her figure the epicranial suture is clearly marked, and its arms are "formed by the lateral edges of the clypeus," she incorrectly homologises the plate in question.

---

* Following C. F. Baker, we may regard *crown* as a less committal term than *vertex*. In the Fulgoroids, moreover, the expressions are certainly not synonymous, since the vertex invades the region commonly known as *front* in these insects.

Posteriorly the crown passes into the occiput without further

Text-figure 1.



Melampsalta leptomera Myers. Face.

fr., front; *c.*, clypeus; *l.*, labrum-epipharynx; *fs.*, frontal suture; *gs.*, genal suture; *fp.*, frontal pit; *oc.*, median ocellus; *mp.*, maxillary plate; *lr.*, lorum.

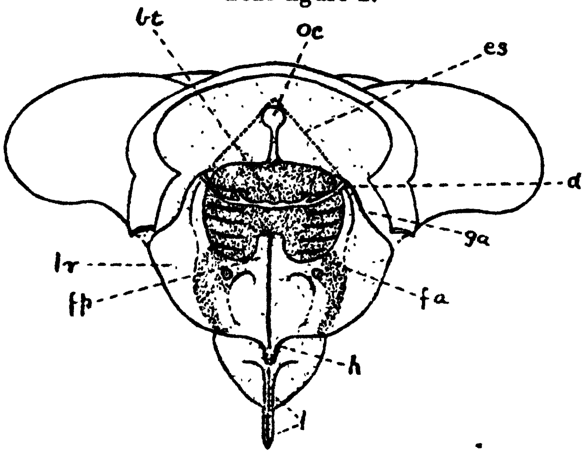
sutures. The paired ocelli are on the vertex just behind the arms of the Y. The compound eyes are large and protruding. The antennæ comprise, as in all other Auchenorrhyncha, a shaft or peduncle and a whip or flagellum. The peduncle has two segments, the first hidden by the horizontal antennal shelf, both simple, lacking sense-organs, and considerably thicker than the first segment of the flagellum. The number of segments of the latter varies within close limits, but in *Melampsalta leptomera* is six. These taper to the apex, though in *Magicicada septendecim* especially the apical one in a fresh condition may be somewhat swollen. Hansen (1890) gives five flagellar segments as normal to the family, but this is an error. The sensillæ, to be described in a later chapter, are confined to the flagellum.

---

* "Morphology and Biology of the Membracidæ of Kansas," Kans. Univ. Sc. Bull. xviii. pl. 11. fig. 35, p. 86 (*Entylia*).

The lower margin of the frons passes into the clypeus (text-fig. 1, *c.* & text-fig. 6, *c.*), with well-defined demarcation from that sclerite. The clypeus is considerably flatter, with a more or less membranous structure arising from its inner surface and projecting as a narrow grooved flap beyond its truncate apex. This structure—the labrum-epipharynx (text-figs. 1 & 2, *l.*)—is throughout grooved on its inner surface for the reception of the mandibular and maxillary setæ, which lie basally between it and the closely-appressed groove of the hypopharynx (text-fig. 2, *h.*). The distal portion of the labrum-epipharyx protects the setæ at the base of the labium, where the dorsal trough of the latter is shallowest.

Text-figure 2.



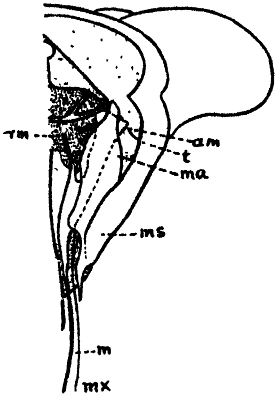
Melampsalta leptomera. Occipital view of head, KOH preparation, trophi removed. *bt.*, body of tentorium; *es.*, epicranial suture; *dt*, dorsal arm of tentorium; *ga.*, genal apodeme; *fa.*, frontal apodeme; *h.*, hypopharynx; *fp.*, frontal plate; *lr.*, lorum (maxillary plates removed); *l.*, labrum-epipharynx; *oc.*, median ocellus.

On each side of frons and clypeus is a crescentic lorum occupying most of the true genal area in cicada (text-fig. 1, *lr.*). Lateral to this in turn is a longer plate, which it largely hides from facial view. This is the maxillary plate (text-fig. 1, *mp.*), which apically meets the free extremity of its fellow to form with it and the labrum a narrow pore through which the setæ pass into the rostral furrow.

Between lorum and frons is the frontal suture (text-fig. 1, *fs.*), which passes up to the crown. Separating lorum from maxillary plate is the genal suture (*gs.*), which almost joins the frontal suture posteriorly.

The sutures mark the external lines of deep flange-like apodemes (text-fig. 4, *a*), the first clear interpretation of which

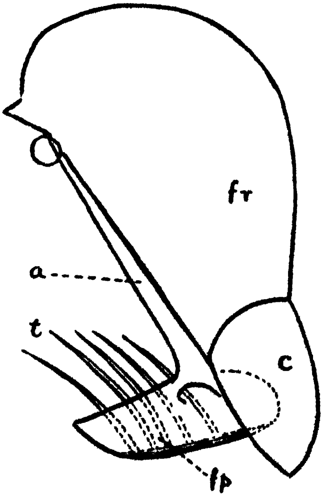
Text-figure 3.



Melampsalta leptomera. As text-fig. 2, but trophi in place.

rm., retractor of mandible; *am.*, articulation of mandible; *ms.*, maxillary plate; *m.*, mandible; *mx.*, maxillary seta; *t.*, tendon of Meek; *ma.*, maxillary apodeme.

Text-figure 4.



Melampsalta cingulata (Fabr.). Exuvial head of ultimate nymph.

a., frontal apodeme; *fp.*, frontal plate; *fr.*, front; *c.*, clypeus; *t.*, tendons of pharynx dilator muscles.

has been given by Muir (1926). The frontal apodeme is narrow near the antenna, but widens apically till it reaches the junction of the frons and clypeus, where it forms a strong strut at a point marked on each side of the face by a deep pit. Surely these pits (text-fig. 1, *fp.*), situated exactly at the junction of the plates we are calling *frons* and *clypeus*, are homologous with the frontal pits of the cockroach and other orthopteroids, and, as such, good landmarks for the recognition of these two sclerites. They may be taken as additional grounds for Muir's supposition that the struts in question are homologous with the anterior arms of the tentorium. These struts flatten out and join in the middle line to form the posterior portion of a deep, trough-like, strongly-chitinized structure which all previous workers before Muir (1926) appear to have regarded as the floor of the pharynx, for which, however, it is only the support, since Muir found in a nymph just after ecdysis that the pharynx can be separated completely as a membranous tube lying on the floor of this trough (text-fig. 4, *fp.*). I have been unable to achieve this separation myself in nymphs or adults, but I had none near ecdysis. This boat-shaped trough is then in its relationship strikingly similar to the frontal plate of the tentorium in some orthopteroids, and should certainly be regarded as homologous therewith. Smith (J. B., 1892) regards it as the mentum!

The genal suture forms internally a similar apodeme, the anterior portion of which joins its fellow from the opposite side to form an anterior support for the ventral wall of the pharynx.

The dorsal arm of the tentorium—nearly always hitherto (Snodgrass; Muir and Kershaw, 1911; Doering, Funkhouser) considered the anterior—arises from (Muir says *near*) this genal apodeme just at its approximation to the frontal apodeme and near the base of the antenna (text-fig. 2, *dt.* & text-fig. 3). It joins the body of the tentorium near the middle. This latter is a short transverse rod, conspicuous in occipital view, swollen near each end at the junction with the dorsal arms, and attached to the apices of the maxillary apodemes. Thence the tentorial body is connected to the outer wall of the head-capsule by an invagination at the ill-defined labial suture of Muir (1926), this invagination possibly corresponding with the posterior arm of the tentorium.

> "At the base of the free apical portion of the maxillary plate on the underside is the opening of the deep invagination which forms the large maxillary apodeme." (Muir.)

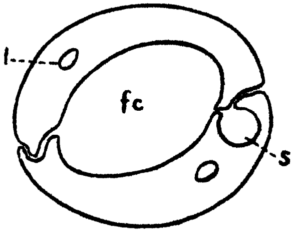
The genal apodeme joins it, and the two form a pouch in which lie the mandibular and maxillary setæ.

The mandible is represented solely by a long stout seta (text-fig. 3, *m.*) of the outer pair and its fairly simple base. This base consists essentially of a moderately wide plate "bent over at the top," to use Snodgrass's (1921 *a*) expression, and connected with the wall of the head-capsule near the upper corner of the frons and the origin of the dorsal arm of the tentorium. On this plate are inserted the protractor muscles, which are attached to the lower portion of the face, chiefly of the lora. The retractor muscles are inserted at the bulbous portion of the mandible where the seta passes into the wide plate, and are attached to the crown behind the ocelli. The mandibular setæ are barbed at the tip, and together loosely enclose the tightly-conjoined maxillary setæ within the rostrum.

The maxilla base is carried further back into the head-capsule than that of the mandible. The protractors attach chiefly to the lower part of the maxillary plate, while the retractors go to the vertex near the attachment of the mandibular ones. The maxillary setæ are finer and intimately locked together, forming a water-tight tube which is split with difficulty and has often been described (*e. g.* Buckton) as one piece, and which lies in the loose channel between the apposed mandibles.

The maxillary setæ are connected by tongues to form this tube, as seen in cross-section (text-fig. 5) in *Fidicina*. The central tube is bounded on all sides by the inner walls of the maxillary setæ (*fc.*), but the section shows there are three holes enclosed in the walls of the canal thus formed. Two—one placed excentrically in each seta—are small, and are the lumina of these organs, allowing passage of nerves and tracheæ, which stand out as fine hairs when the maxillary setæ are cut. The third passage is larger, and is formed by a deep nearly enclosed groove in one seta roofed over by the apposition of its fellow. The large central canal is, of course, for the passage of food, and the parietal channel for that of saliva. In *Graphosoma*, and apparently in most other Heteroptera, the two canals are more nearly equal, the salivary passage being slightly smaller.

Text-figure 5.



Fidicina semilata (Wk.). Cross-section of maxillary tube.
fc., food-canal; *s.*, salivary canal; *l.*, lumen of one maxillary seta.

The setæ are capable of considerable extension beyond the tip of the labium (text-fig. 68).

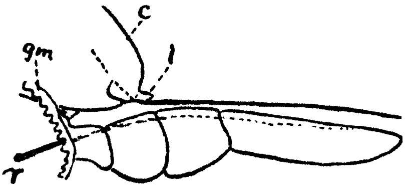
The hypopharynx is a pad-like triangular structure grooved for the reception of the setæ and fitting closely against the inner surface of the epipharynx. Below the terminal portion of the hypopharynx is a swelling containing the salivary pump, described more fully in the account of the alimentary system.

This terminal part is fused with the chitinous plate supporting the ventral wall of the pharynx. The lateral wings of the hypopharynx seem to be directly continuous with the lora, as noted by Snodgrass (1921 *a*) and seen in text-fig. 2 (*h.*, *lr.*)—an extremely anomalous condition. Possibly the term *hypopharynx* is to be restricted to the terminal somewhat spoon-shaped portion, as held by Muir and Kershaw (1911 *a*, p. 5).

The labium forms the rostrum or sheath for the setæ. It is attached by feebly-chitinized membrane, and, as noted by Meek, shows stronger connections with the prothorax than with the head—a condition developing early in embryonic life (Heymons, 1899). In its distal portion the labium is a deep, trough-like, almost closed tube. Three segments are recognizable with signs of a fourth (text fig. 6). From the proximal segment the chitinized floor of the labial groove becomes differentiated as a free chitinized rod (text-fig 6, *r.*) for the insertion of the muscles of the labium.

Bugnion and Popoff say that in the Pentatomoid, *Graphosoma lineatum* (1911, p. 651), the labial canal forms, near the tip at least, a completely closed tube. Above this (proximally) the groove is open to permit the labium to bend away from the setæ and allow penetration, the flexion occurring between the first and second labial segments. They note that, if the setæ by accident are drawn entirely out of the labial trough so as to escape from the closed apical tubular part, the bug is unable to return them and dies of starvation. We doubt whether this condition is at all general, and we have shown in the New Zealand Pentatomid, *Rhopalimorpha*, that when the setæ are penetrating to the fullest extent, the labium is withdrawn from them completely and folded back along the venter*.

Text-figure 6.



Melampsalta leptomera. Rostrum of ultimate nymph.

c., clypeus; *l.*, labrum-epipharynx; *gm.*, gular membrane; *r.*, chitinized rod.

In cicadas, at least in *M. cingulata*, the apical portion of the labial groove is not shut. The shortening of the labium to allow penetration of the setæ takes place by wrinkling transversely in the terminal segments.

---

* "The Feeding-habits of Hemiptera," New Zealand Journ. Sci. & Techn. iv. pp. 265–266, figs. 1–3 (1921).

The mechanism of the mouth-parts is so linked up with the functioning of the salivary glands and pharynx that it has been dealt with under the physiology of the digestive system. The chief point to emphasize is the presence of a distinct salivary canal in the wall, as it were, of the much larger food-channel. This has been frequently overlooked (*e.g.* Snodgrass, 1921 *a*). The setæ can be pushed out by the approximate muscles with considerable force, even in alcohol specimens.

β. *Notes on the Homologies.*

Smith (1892) considered the whole mandible to be represented by the lorum, while both setæ were derived from the maxilla, as also were the maxillary plate and the labium! He seems to have strained his interpretation to accord with *a priori* conceptions drawn from a study of the Dipterous condition. In more detail he homologized the maxillary plate with the palpus, the rostrum with the subgalea+galea, and the two setæ with the lacinia and stipes respectively.

Marlatt (1895) considered our frons the clypeus and our labrum-epipharynx the labrum or rather part of it. The lorum was considered a "mandibular sclerite" bearing the same relation to the mandibular seta as the maxillary plate or sclerite to the corresponding seta—a view still much held in some quarters, *e. g.* Comstock.

Meek (1903) did a very detailed piece of work, and was one of the few cicada workers to notice the salivary canal. He considered the frons to be correctly homologized. Marlatt was followed regarding the "mandibular sclerite" or lorum.

Just before Meek, Bentley (1900) considered the frons, in our sense, the clypeus.

Berlese (1909) studied both the nymphal and adult heads, but adopted a terminology which has few adherents. Our *vertex* is called the *post-front*, while our triangular appendage of the frons bearing the median ocellus is the tergite of the antennal or second head-somite, of which the sternite is constituted by the antennal shelf (p. 86, fig. 41). Unfortunately, the different sections of Berlese's tremendous work are not always consistent *inter se*, so that, for instance, our frons, usually called by Berlese *prefronte* (p. 86, fig. 41) on fig. 422, is labelled *clypeus*. The adult head is considered more especially on pp. 98–99, figs. 58-60, where the clypeus is so labelled, except a small and not really differentiated portion which is called *labrum*, our labrum-epipharynx not appearing in any of his figures, having been probably boiled off in caustic potash. The labium is said to consist of *submentum*, *mentum*, and appendages (*lobi*). The hypopharynx is considered (p. 355) to form the floor of the labial gutter, and to be produced backward into the head as a peculiar process, which is evidently our text-fig. 6, *r*.

Muir and Kershaw (1911 *a*) considered adult structure. They recognized and pointed out the importance of our frontal suture, called "mandibular suture," and described the mandible articulating by a "true ginglymus articulation" at the posterior end of this suture. The articulation point is taken as a landmark between frons and clypeus, and our present frons is therefore designated *clypeus*. A very good and clear account of the mechanism is appended.

The same writers (1911 *b*) made embryological studies on a Reduviid Heteropteron, demonstrating, as Heymons (1899) had already somewhat indefinitely indicated, that the mandibular seta and its actual base develop from the entire mandible. At the same time they confirmed Heymons's demonstration of the early differentiation of the maxilla into maxillary plate and seta.

A third paper by these authors (1912) considered the nymphal head of the cicada and the embryology of the *Siphanta* (Flatidæ) head. The results confirmed those previously announced.

Snodgrass (1921 *a*) gave a very clear and beautifully illustrated account of the head of *Septendecim*, with a critical discussion of previous work, making also a suggestive comparison with an Acridian head. He considered the frons to be homologized as we have stated, and called our labrum-ephipharynx the labrum. The salivary channel of the maxillary setæ was missed entirely.

The same writer (1927), influenced by his new decision that the second enlargement of the food-canal is the true pharynx, believes that the frons should be known as the *post-clypeus*, and the clypeus, in our sense, the *ante-clypeus*—a view in which we cannot follow him, but which is discussed in the account of the food-canal.

Muir (*in litt.*, and in 1926) now believes that our frons should be so-called, or perhaps *clypeo-frons*. The chitinous piece supporting the posterior half of the pharynx or sucking-pump is compared with the frontal plate of some Orthoptera, and is shown to be tentorial rather than stomodæal in origin.

The chief debated points in the literature thus reviewed concern the homology of the large, striated, facial sclerite, and with it that of all the other pieces of the face, and, secondly, the interpretation of the tentorial structures. If the chitinous trough which supports most of the sucking-pump is, as Muir suggests, the frontal place of the tentorium—to which it was compared also by Snodgrass (1921, p. 2),—then the strut connecting it with the rest of the frontal apodeme marks the invagination of the anterior arm of the tentorium. And as this invagination is generally accepted as marking the boundary between frons and clypeus, the striated facial sclerite would be the frons. This was the view of Snodgrass (1921 *a*) and of Meek. In Heteroptera, Bugnion and Popoff (1911, p. 650) would seem also to agree when they state "plus en arrière, les bords de l'épistome (clypeus) forment deux petits ailerons (figs. 2, 3, *ai.*), qui donnent attache par leurs angles postérieurs aux branches antérieurs du tentorium...." But they believe the facial sclerite in question to be the clypeus (*épistome* or *chaperon*).

because it gives insertion to the pharyngeal dilator muscles—"une des caractéristiques du clypeus est qu'il donne insertion par sa face profonde aux fasceaux antérieurs du dilateur du pharynx." Yet Snodgrass (1921, p. 1) calls the same piece the frons for exactly the same reason that the French writers named it *clypeus*. "The prominent ridged facial plate (*Ft.*) is designated the *front* because of the attachment of the pharyngeal muscles to it as in other insects." The clypeus of the two French workers would therefore appear to be the front of general morphologists. Snodgrass, however, believing now that the true pharynx is the second enlargement in the alimentary canal of cicada (see section on digestive system) and that his "pharynx" of 1921 is a modified mouth-cavity, has changed his views on the homology of the striated sclerite accordingly, and identifies the true front with the small triangular piece bearing the median ocellus and considered by us a part of our frons, which Snodgrass now considers largely clypeal, as did Muir and Kershaw (1911, 1912). But in the meantime Muir has decided that he was mistaken in his former views on the tentorium, and now advances the views set forth at the beginning of this paragraph, according to which the disputed striated sclerite is the frons. Thus, curiously enough, Muir and Snodgrass have in a sense changed places in their interpretation.

We have seen that Snodgrass now regards the great sucking-pump as a modified part of the mouth-cavity rather than a true pharynx, since is has no general muscular covering, but only the dorsal dilators. But granting, as we must, that this sucking-pump is analogous in function to that of non-Hemipterous insects, the loss of transverse muscles and the great development of dorsal dilators are perhaps not sufficient reasons for declining, with Snodgrass, to regard it as also homologous in structure. At least it shows no greater modification than the trophi themselves, if, as all agree, these also were derived from the homologous parts of a mandibulate insect. Moreover, we may ask what constitutes a pharynx other than the anterior portion of the stomodæum. The demarcation between mouth-cavity and pharynx, and between this and œsophagus, is surely more or less arbitrary.

If Muir's present view as to the tentorium be correct—and it would be difficult to explain the condition found in text-fig. 4 on any other basis,—then the anterior arms of the tentorium in the previous sense of Muir and Kershaw (1911, 1912) and in that of Doering (1922) really correspond to the dorsal arms in the cockroach and other insects. The likelihood of confusing these two pairs of arms was pointed out by Dr. Crampton in conversation.

Muir makes the interesting suggestion that the elements of the tentorium represent segmental apodemes, arising at the edge of the segments composing the head. In cicada there are four pairs of such invaginations—frontal, genal, maxillary, and labial.

Labrum-epipharynx.—The projecting portion, or the whole, of this terminal sclerite of the face has been called the *labrum* by most of those who identify the large, striated, swollen plate as the frons (Snodgrass, 1921; Meek, and Tower in Heteroptera), and epipharynx by those who name the directive sclerite the clypeus. Meek would distinguish a rudimentary labrum, deeply grooved and overlying the epipharynx. Muir and Kershaw (1911 *a*, p. 2) suggest that the division between labrum (our clypeus) and epipharynx is not distinct, and therefore the piece might be called *labrum-epipharynx* as in Diptera. But with the homology suggested in the present contribution the compound term might, for the following reasons, be retained for the narrow terminal piece only. If it arose from the edge of the sclerite which we call clypeus, it would be a simple labrum: but its origin on the inner surface (text-fig. 2, *l.*) of the clypeus and its general nature as a grooved pad, save distally, are epipharyngeal characters. Yet the epipharynx, in Insecta generally, arises from the inner surface of the labrum, not of the clypeus (Comstock, Imms), though Packard (1898, p. 43) states: "The epipharynx is the under surface or pharyngeal lining of the clypeus and labrum, forming the membranous roof of the mouth." In these circumstances we think it advisable to retain the compound name for the terminal sclerite of the cicada face.

With regard to the embryological development of the trophi, a word here must be said of Heymons's (1899) contribution, dealt with fully in a later section. Comstock (1925, p. 398) quoted Heymons in support of the view that the "mandibular sclerites" (our lora) are formed from the basal part of the embryonic mandible, while Snodgrass (1921, p. 8) brings him in as proving the contrary. It behoves us, therefore, to see what Heymons really stated on this question. He did definitely prove that the maxilla split early into a plate and seta, or rather into two lobes giving rise respectively to these structures: but concerning the mandibles he was less definite. The following pasage (Heymons, 1899, p. 422) is doubtless Comstock's witness:—

> "Da die Lora bei den Homopteron selbständige, deutlich von der Stirn abgegrenzte Sceletstücke sind und da sie im derselben Beziehung zu den Mandibeln stehn wie die Laminæ max. zu den vorderen Maxillen, so können die 'Lora' entsprechend als Laminæ mandibulares bezeichnet werden."

But Heymons evidently wished to regard the "mandibular sclerite" as homologous with the maxillary plate, though his own embryological work and figures indicate no such correspondence. Thus (1899, p. 422):—

> "Diese sog. Lora sind in entwicklungsgeschichtlicher Hinsicht keine ganze einheitlichen Bildungen, indem sie sowohl auf Bestandtheile des Antennensegmentes wie auf solche des Mandibelsegments zuruckzufuhren sind."

And further (p. 440):—

> "Vom anatomischen Standpunkte lassen sie sich deswegen mit den Laminæ maxillares vergleichen, weil sie wie diese die Insertionsfläche für die Protractormuskeln (Mandibulare Protractoren) enthalten. Entwicklungsgeschichtlich habe ich dagegen nicht den Nachweis führen können, dass an dem Aufbau der Laminæ mandibulares sich auch noch die Extremitäten des Mandibularsegments betheiligen" (p. 438). "Die Mandibel würde demgemäss also im wesentlichen nur noch die morphologische Bedeutung einer 'Lade' besitzen."

In view, therefore, of Muir and Kershaw's work, it may be taken as established that the whole of the embryonic mandible develops into the seta and its base.

To sum up this section, we may regard three other points in cicada head morphology as settled:—

(2) That the sclerite on each side, which we have called the lorum, is a part of the gena, and is neither a lateral development of the clypeal region, as Muir and Kershaw (1911 *b*, p. 78) believed, nor the sole remains of the functionless mandible (Smith, 1892), nor yet a mandibular sclerite (Meek, Marlatt, and others). In this interpretation Muir, according to his latest paper (1926), agrees with Snodgrass.

(3) That the maxillæ are represented on each side by a basal plate which becomes more or less fused with the head-capsule, and a distal seta which with its fellow forms the second or inner pair of rostral setæ. This follows from the embryological work of Heymons and of Muir and Kershaw, and as Snodgrass (1921 *a*, p. 8) has said, must be accepted until new embryological evidence is adduced to the contrary.

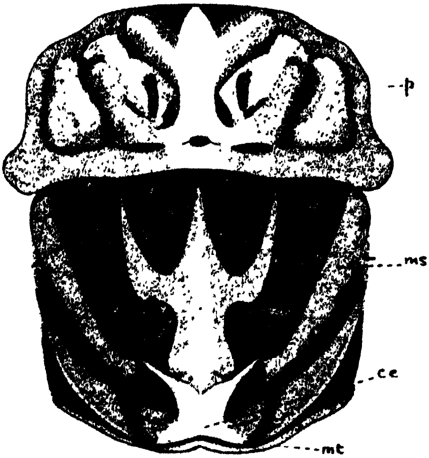
(4) "All writers, except Smith," writes Snodgrass, "agree that the labium of the adult is formed from the fused labial appendages of the embryo." Muir would call the basal segment in cicada the *mentum*, the second, which is somewhat swollen, the *palpiger*; and the third the *ligula*. Berlese (1909) terms the same segments *submentum*, *mentum*, and *lobi*, while Marlatt (1895) calls them *submentum*, *mentum*, *ligula*.

d. THORAX AND ITS APPENDAGES.

α. *Thorax*.

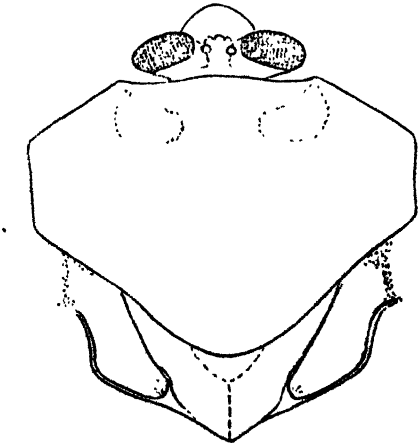
As in so many other characters, there is considerable homogeneity in thoracic structure throughout the family. A noticeable feature is the greatly enlarged mesothorax and especially its notum, doubtless associated with the very stout and powerful fore-wings or tegmina. In the nymph, on the other hand, the prothorax, carrying the musculature of the strong fossorial fore-legs, is much the largest of the thoracic segments; and such is the condition in the imago of *Tettigarcta*, where the hypertrophied pronotum (text-fig. 8) overshadows the much

Text-figure 7.



Melampsalta muta (Fabr.). Thoracic nota.
p., pronotum; *ms.*, mesonotum; *mt.*, metanotum; *ce.*, cruciform elevation (scutellum).

Text-figure 8.



Tettigarcta crinita Dist. Head and nota showing the tremendously enlarged pronotum.

reduced mesonotum. In this primitive form the tegmina are far weaker, without that massing of veins on the fore-border so characteristic of all other cicadas. In these latter, however, the pronotum is the second largest of the thoracic segments (text-fig. 7, *p.*).

The only worker to deal especially with thoracic structure in Cicadidæ is Taylor (L. H., 1918) who used *Tibicen linnei* S. & G. (*Cicada tibicen* nec L.) and *Cryptotympana epithesia* Dist.

Berlese (1909) gives considerable details.

Our description and figures are based largely on *Melampsalta cingulata* and *M. muta*.

Three pairs of small, free, cervical sclerites are present.

In the prothorax the notum is curved down considerably laterally. The surface is marked with deep grooves associated with muscle insertions, though Taylor would regard them as division marks for a triangular prescutum, a scutum narrow mesally and wider as it approaches the pleuron, and a scutellum. We believe this to be entirely fanciful, as, indeed, Crampton * has indicated in *Dissosteira* (p. 350) when he says that the sulci of the pronotum divide the surface into areas which have been very incorrectly identified as *prescutum*, *scutum*, etc., although they are purely secondary structures having no connection with the typical notal subdivisions of the wing-bearing segments.

The pleuron of the prothorax is greatly reduced and practically fused with the notum. The fusion concerns chiefly the epimeron, while the episternum is more reduced.

The prosternum is represented by a single plate bearing the well-developed furca of the endoskeleton. The plate may be regarded as a fused eusternum and sternellum.

The mesothorax, as we have seen, is the largest division of the thorax. The anterior part of its notum projects beneath the pronotum almost to the occiput, and this part has been distinguished by Taylor as the anterior phragma (*prophragma* of Berlese). The prescutum is only indefinitely marked off by sutures beginning along the outer edges of the dark obconical marks which form an almost constant feature of cicada markings (text-fig. 7). These correspond to muscle insertions. The greater part of the notum is occupied by the scutum, but the scutellum is sharply differentiated as the *cruciform elevation* of taxonomists (*ce*). The posterior edge of the scutellum runs down laterally to give insertion to the axillary cord of the tegmen. The scutellum entirely hides from dorsal view the strongly-chitinized post-scutellum or post-notum, which forms a shelf beneath it. The post-scutellum is joined to the epimeron by a narrow bridge (text-fig. 9, *poa.*) called by Taylor the *postalare*, which is just the prolongation of the katepimeron.

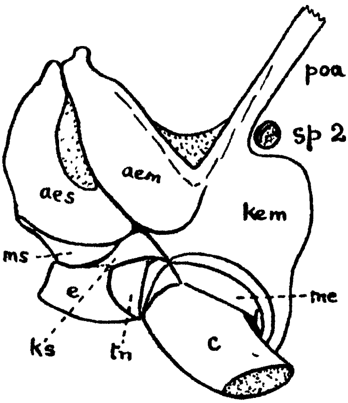
On the pleuron the pleural suture is distinct, and in addition there is a suture dividing the episternum into an upper anepisternum (*aes.*) and a lower katepisternum. The latter suture is continuous posteriorly across the pleural suture, and there divides the epimeron in the same way, a condition said to be peculiar to the Cicadidæ. At the lower extremity of the pleural suture the coxal region shows a distinct posterior meron (*me.*) and true coxa (*c.*). In *Cryptotympana* Taylor found that a median portion was marked off on the episternum between what we have called *anepisternum* and *katepisternum* respectively, and this tripartite condition recurs in *Melampsalta* (*ms.*). It will be interesting to study its occurrence throughout the family.

---

* "The Thoracic Sclerites of the Grasshopper, *Dissosteira carolina*," Ann. Ent. Soc. Am. xi. pp. 347–366, pl. 32. text-fig. (1918).

In the mesosternum of *Melampsalta* a eusternum or basisternite (*e.*) and a sternellum or furcasternite are to be distinguished. The invagination in the latter to form the furca presents externally a deep and wide mouth. The trochantin (text-fig. 9, *tn.*) is normal.

Text-figure 9.



Melampsalta sericea (Wk.). Mesopleuron.

aes., anepisternum; *aem.*, anepimeron; *ms.*, median division of episternum; *e.*, eusternum; *tn.*, trochantin; *c.*, true coxa; *ks.*, katepisternum; *kem.*, katepimeron; *me.*, meron; *poa.*, postalare; *sp.* 2, second spiracle.

The metathorax is extremely short, especially dorsally, where the whole notum is reduced to a narrow band (*mt.*) behind the scutellum of the mesonotum. The posterior edge runs down laterally to the axillary cord of the hind wing.

In Taylor's two species and in *Melampsalta* the pleuron shows a distinct pleural suture dividing off an anterior episternum (*es.*) and a posterior epimeron (*em.*), both of which remain undivided further (text-fig. 10). Taylor (p. 232) writes:—

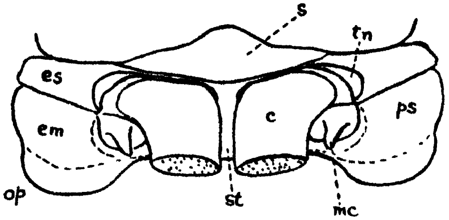
> "The epimeron of the female is large and rectangular. In the male a broad lobe, called sometimes the operculum, extends backward from the epimeron and sternum. . . . ."

We believe that the operculum is purely epimeral. In *Septendecim* it may be seen distinctly to curve round the posterior margin of the sternum, towards its fellow. Moreover, the sternum has a distinct process of its own to which the folded membrane is attached. We shall discuss these structures in more detail in connection with the rest of the sound-producing apparatus.

The metasternum shows a eusternum (text-fig. 10, *s.*) and a sternellum (*st.*). The trochantin occupies its usual anterior position (*tn.*), and must not be confused, as is so often done, with the meracanthus (*mc.*) of Fieber, which is a spur arising from the meron.

Thoracic Endoskeleton.—The furca of the prothorax is very strongly developed, the others less so. The chief peculiarity of the endoskeleton is the great development of the mesophragma, giving insertion to the great lateral muscles of the mesothorax (*costali-dorsali* of Berlese). This phragma is called by Berlese the *preclavicola del metanoto.* But it seems to us to arise distinctly from the postnotum of the mesothorax, and thus to be a postphragma of that segment. Taylor (p. 230), with views evidently coloured by Berlese, writes of the post-scutellum or post-notum as "fused with the anterior phragma of the metathorax," but gives no evidence that the phragma in question belongs to the metathorax rather than to the mesothorax. We may, of course, beg the question by admitting that in the last analysis, since a phragma is a plate invaginating *between* segments, it belongs to neither. But Crampton, in his work above cited on *Dissosteira*, makes the definite statement (p. 354) that the post-scutellum of the metathorax *bears* a phragma for the attachment of the longitudinal muscles arching the notum in the movements of flight; and similarly, in an earlier paper *, "The posterior plate .... or post-scutellum usually consists of an external region bearing an internal phragma."

Text-figure 10.



Melampsalta muta. Female: metasternum etc.

s., basisternite (eusternum); *ps.*, pleural suture; *mc.*, meracanthus; *es.*, episternum; *em.*, epimeron; *op.*, operculum; *st.*, sternellum; *c.*, coxa; *tn.*, trochantin.

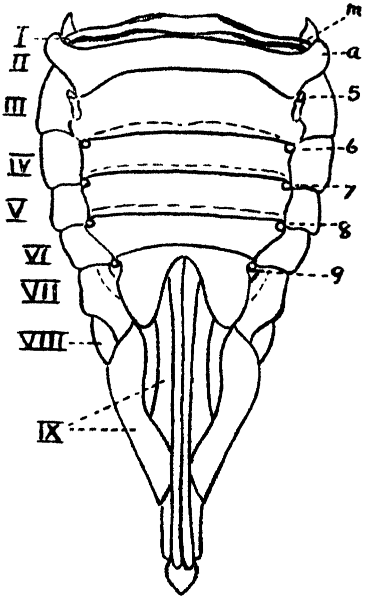
Imms, moreover (1925, p. 47), would appear to hold the same opinion. We therefore name as mesophragma the great plate which cuts off the whole of the fore-part of the body from the metathorax and abdomen, leaving a narrow perpendicular slit for the passage of the viscera and nerves.

---

* G. C. Crampton, Zoologisch. Anzeiger, xliv. p. 60 (1914).

Relationships.—The tripartite mesothoracic episternum is considered by Taylor a neuropteroid character. Crampton has also used thoracic structure as an argument for neuropteroid relationships. According to Taylor the threefold division of the episternum is present also in Cicadellidæ (Jassoidea). The composite mesothoracic epimeron would appear to occur in no other Homoptera.

Text-figure 11.



Melampsalta muta. Female abdomen: ventral view; ovipositor largely disengaged.
I.-IX., abdominal segments; 5-9, spiracles; *m.*, mirror (tympanum of chordotonal organ); *a.*, auditory capsule.

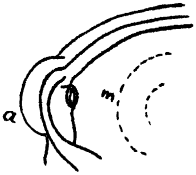
β. Legs.

Hansen has made a detailed study of the legs (1890, trans. 1900–1903).

The prothoracic legs of the Cicadas are highly characteristic both in the nymphal and imaginal stadia. The femora of the first (see later section) are much swollen and strangely modified for fossorial purposes; those of the second (text-fig. 15) are

enlarged almost as much, and furnished ventrally usually with three stout spines, directed somewhat obliquely. The trochantins, as we have seen, are distinct, the coxæ very long, with a considerable distal portion free. The interior angles of articulation are at a considerable distance from the insect's middle plane (Hansen). The trochanters are thick with a very oblique femoral articulation, producing a see-saw movement.

Text-figure 12.

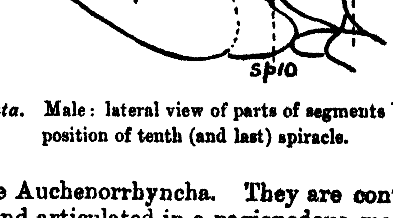


Melampsalta muta. Male: front view of right fourth spiracle. *m.*, mirror; *a.*, auditory capsule.

The second and third pairs of legs are unspecialized, showing a probably primitive simplicity. In the second pair coxæ are moderately short and broad, and situated near the middle plane. Their principal movement is rotary (Hansen). There is no true meracanthus, but the meron is well developed.

In the third pair the coxæ, according to Hansen, are the simplest in the Auchenorrhyncha. They are contiguous in the middle plane and articulated in a pagiopodous manner, *i. e.* only a hinge-movement is possible. The meracanthus is usually well developed.

Text-figure 13.



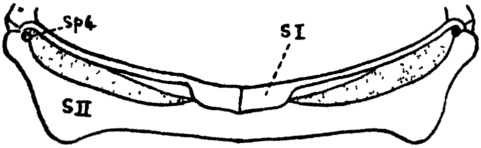
Melampsalta muta. Male: lateral view of parts of segments VII.-IX. to show position of tenth (and last) spiracle.

The tarsi are usually three-segmented as in all other Auchenorrhyncha, but Cicadidæ differ in lacking any empodial formation.

The claws are two—equal, stout, and simple. Those of the nymphs, as first indicated, but not described, by Hansen (transl. 1901, p. 151), are very different from those of the adult.

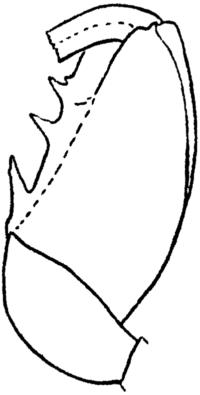
In the universal habit of cicadas to rest habitually in a perpendicular position, whether the support be trees, herbs, or rocks, we may see an explanation of the powerful fore-legs. The attitude is largely a suspensory one, in which the second and third pairs take little part, most of the weight falling on the prothoracic pairs. A similar condition occurs in certain moths.

Text-figure 14.



Melampsalta muta. Female: ventral view of base of abdomen.
sp. 4, fourth spiracle; S.I., first abdominal sternite; S.II., second ditto.

Text-figure 15.



Melampsalta sericea. Fore femur, inner view.

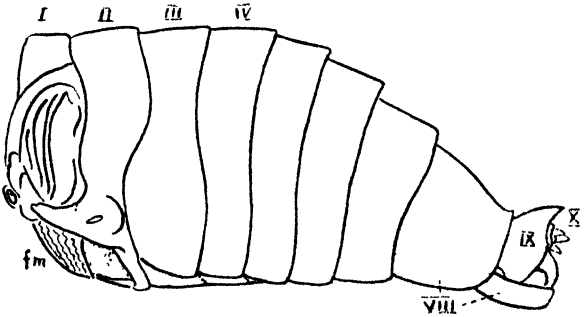
γ. *The Wings.*

Chabrier (1822), Amans (1885, 1915), and Imhof (1901, 1905), also Haupt (1913), have devoted considerable study to cicada wing-structure from the viewpoint of the mechanics of flight. Comstock and Needham (1898), in their first classic attempt to homologize the wing-veins in all the orders, studied cicada venation in detail and ascertained its condition in the nymphal wing. Their interpretation, with the Tillyard modifications, has been adopted in this paper. Woodworth (1906) dealt more or less incidentally with cicada venation, and drew attention to the nodal line, missed by Comstock and Needham (at least in text), but considered at greater length by Horváth (1913) in a paper which introduces several divergences from the Comstock-Needham interpretation. Berlese (1909) pays considerable attention to the axillary sclerites.

The first taxonomic division of the family was based, unsuccessfully as events have proved, on the wing-venation, while later workers have used it for generic separation.

Comstock's latest account (1918) is apparently identical with that of Comstock and Needham's original contribution, while Moulton's account (1923) and figure follow Horváth. Comstock's type was *Tibicen*; ours will be chiefly *Melampsalta muta*, with which we have attempted to compare other members of the family. Text-figs. 49, 50, and 53 are to the same scale, while 48 and 54 are more enlarged.

Text-figure 16.



Melampsalta sericea. Lateral view of male abdomen.
I.–X., abdominal segments; *fm.*, folded membrane.

i. *Tracheation.*

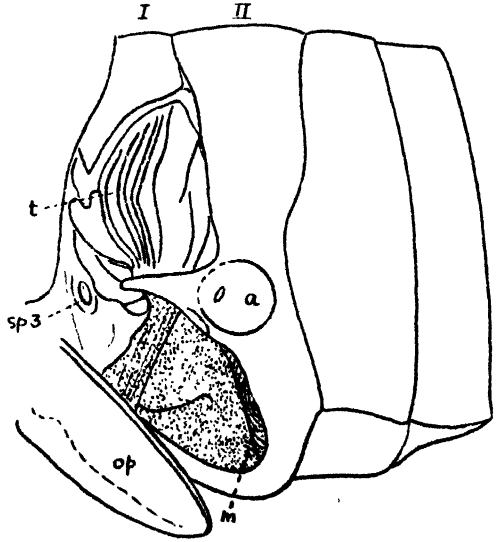
A transverse basal trachea exists between the costo-radial and the cubito-anal groups of pre-venational tracheæ in the developing wing-base. In this respect cicadas are less primitive than Membracidæ, Cercopidæ, and some at least of the Cicadellidæ, where the basal connection is absent—a condition that exists nowhere else according to Comstock (1918, p. 275), but in Plecoptera and certain Blattids. Comstock has shown that when this transverse basal trachea is present the medial trachea tends to migrate along it towards the orbit-anal group. This is well shown in cicadas, and reaches an extreme in those cases where the M and Cu are united in a common stalk a considerable distance after entering the tegmen (text-figs. 48, 49; *cf.* 50, 55).

The tracheation is of the simple type, in which only the principal veins are represented by pre-existent tracheæ. The nymphal scheme is much more primitive than the adult venation would lead one to suspect, and, in fact, it approaches very closely to the Comstock-Needham hypothetical type. The great reduction of R 1 is a striking difference.

ii. *Venation.*

In the following interpretation we have followed, in company with Muir, Imms, Alexander, and many other workers, the Tillyard modification of the Comstock-Needham system, considering the latter's 1 A to be really Cu 2.

Text-figure 17.

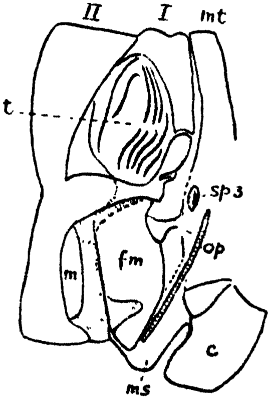


Melampsalta muta. Male: lateral view of left sound-apparatus.
t., tymbal; *sp.* 3, third spiracle; *op.*, operculum; *a.*, auditory capsule; *m.*, mirror.

First is a description of the venation in *Melampsalta muta*, and then a discussion of divergences in other members of the family. The orthodox abbreviations need no explanation.

In the tegmen (text-fig. 48) there is a conspicuous massing of veins on the costal margin; but the elements are distinguishable under magnification. Costa is very thick and coincides with the margin of the wing. Sc is fused with R, at least as far as the nodal furrow, which will engage much of our attention later. R 1 is apparently obsolete in the imago. The fate of the other branches will be apparent from text-fig. 48 (*cf.* 49, 50). The base of M is in close contact, if not actually united, with the common Sc + R stem until the arculus is reached. There M splits off to form the anterior arculus and to join Cu, by which latter fusion the posterior arculus, seen in more typical cicadas (e.g. *Tibicen*, text-fig. 55) and representing the cross-vein between M and Cu, is obliterated. So far we are in accord with Comstock and Needham, save for the differences in the species described. These writers state that there is a peculiar and unparalleled condition in certain insects, including cicadas, consisting in the fusion of 1 A with the base of Cu, so that it appears a branch of Cu, far separated from the common stem of 2 A and 3 A. Tillyard has given good reasons for considering their 1 A as Cu 2, thus making Cu two-branched—a far more probable explanation of the condition. The anal furrow lies along the conjoined courses of Cu 2 and 1 A.

Text-figure 18.



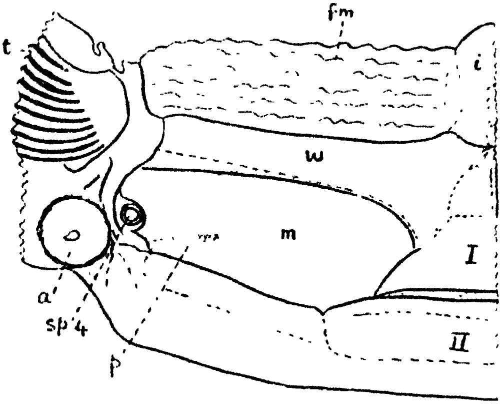
Melampsalta sericea. Male: lateral view of right sound-apparatus, with segments softened and stretched to fullest extent.

op., cut base of operculum; *c.*, metacoxa; *fm.*, space normally covered by folded membrane; *ms.*, metasternum; *mt.*, metanotum. Other letters as in text-fig. 17.

The venation of the hind-wing is more specialized than that of the tegmen, the difference depending, in Comstock's opinion, on the more nearly basal forking of R in the former. From this it results that only R 2 + 3 fuse for a considerable distance with Sc (R 1 being completely lost), while R 4 + 5 coalesces for a short distance with M. The common Sc + R 2 + 3 stem is in close contact with C, and in *Tettigarcta* (text-fig. 53) seems actually fused with it. While M is normally only three-branched, there occur aberrations in which exists a small remnant of cell M 2, usually crowded out by coalescence of M 2 and M 3 as in our figures. This venational variation is only one of many which occur with frequency in all genera of which I have seen sufficient material for comparison, and such characters should be introduced with great circumspection into taxonomy, even when they appear constant. *Pauropsalta*, founded by Goding and Froggatt on such a venational difference, I do not think can stand, and Bergroth (1911) has been critical of some of Distant's similar characterizations.

Applying the Tillyard correction in the hind wing, we find in the adult (text-fig. 54) that Cu branches in a U-shape right at the base of the wing, and the two branches become considerably separated, Cu 1 dividing into Cu 1*a* and Cu 1*b*, while Cu 2 runs in the anal furrow with, but really separate from, 1 A. The two remaining veins, by this interpretation, are 2 A and 3 A respectively, thus being avoided the anomalous attribute of four anal veins, or a two-branched 3 A, required on the Comstock hypothesis. The anal area is much more developed in the hind wing than in the fore, and folds under the corium when at rest.

Text-figure 19.



Magicicada septendecim (L.). Male: KOH preparation of mirror and adjacent parts, flattened out.

fm., folded membrane; *i.*, intersegmental membrane between thorax and abdomen; I., II., abdominal sternites; *m.*, mirror; *p.*, process to chordotonal organ; *t.*, tymbal; *w.*, wing (see p. 466); *a.*, auditory capsule.

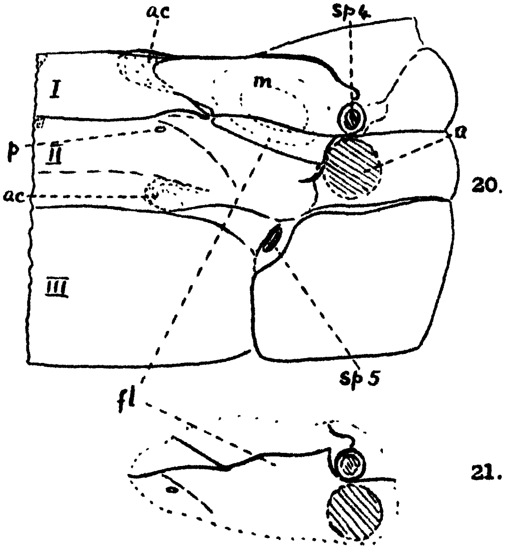
Finally, both tegmen and hind wing are surrounded by a strong border between the ambient vein (text-fig. 48, *amb.*) and the edge of the wing.

Venation in the Family.—Main features, as described above in *Melampsalta*, recur throughout the family, save in the subfamilies Tettigarctinæ and Tettigadinæ.

Net-veining of the tegmen, a character on which Amyot and Serville based the first classification of the family, has almost certainly arisen independently in several different branches of the family, and occurs to-day in several unrelated genera:—*Polyneura*, *Angamiana*, *Talainga*, *Hemidictya*, and others. The condition, moreover, in such a form as *Polyneura*, brought about by excessive regular dichotomy of the longitudinal veins, differs greatly from the network of irregular cells found in the Hemidictyine forms.

Lembeja (text-fig. 56) and *Cystosoma* show a more or less complete absence of the coriaceous border on the tegmen, the ambient vein coinciding with the margin, which it slightly thickens.

Text-figures 20 & 21.



Magicicada septendecim. Female: as text-fig. 19. Internal view.

ac., vestiges of Vogel's rudimentary abdominal coxites I. and II.; I.–III. abdominal sternites; *p.*, left member of pair of pores of unknown function; *fl.*, flap (see text).

Fig. 21. Portion of the same preparation as in text-fig. 20, but with flap turned forward.

More fundamental differences occur, as we have mentioned, in *Tettigarcta* and in the Tettigadinæ, which show between them a gradation leading up to the specialised condition of the dominant and more typical cicadas. Venationally there is much more in common between *Tibicen* and *Melampsalta*, which are separated as far as possible under the present classification, than there is between either and *Tettigarcta*. Yet the present scheme places the latter with *Melampsalta* in the same subfamily.

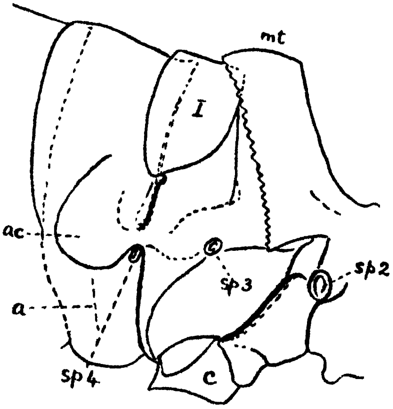
Tettigarcta is at the very base of the Cicadidæ, and is extremely primitive in far more respects than absence of sound-organs, and not least so in venation.

The Tettigadinæ, of which we have examined *Chonosia crassipennis* (text-fig. 49) as a type, connects it, venationally only, with the dominant groups, and so may be described first.

In the first place, *Chonosia* shows a distinct strongly-marked membrane fold along the nodal line, to be discussed later.

Secondly, Cu 2 lies, as usual, in the anal furrow or on the claval suture, but considerably distant from 1 A, both basally and distally, as pointed out in the characterisation of the subfamily by Jacobi (1907 *c*). The strongly-chitinized base of the clavus at the point corresponding with the posterior tuberosity of Amans is said to be strongly developed in the whole subfamily Tettigadinæ, and is supposed to form a plectrum for the stridulating apparatus on the mesonotum (text-fig. 59). In *Chonosia crassipennis* I do not find that it is much more protuberant than in other Cicadidæ, and Mr. W. E. China, from experiments with a softened specimen of a *Tettigades*, expresses grave doubts as to whether this structure could be employed as a plectrum. Unfortunately observations in the field are lacking.

Text-figure 22.



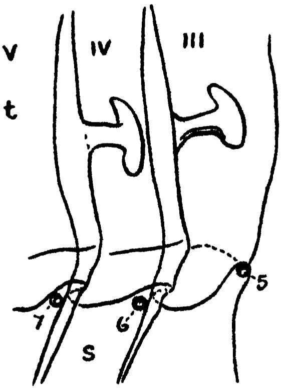
Melampsalta leptomera. Ultimate female nymph: junction of thorax and abdomen extended to fullest extent. Lateral view, right side.

mt., metanotum; *sp.* 2, second spiracle: *ac.*, region of future auditory capsule; *a.*, region which in male develops future tymbal; *c.*, metacoxa.

In *Tettigarcta* (text-fig. 50) the whole tegmen is markedly coriaceous, the basal half especially so. The surface is covered with irregular shiny tuberculations. The nodal line is extremely distinct, as well on the membrane as on the veins themselves.

The anal furrow is very deep, the vein Cu 2 on its floor rather weak. The ambient vein is normal, but the coriaceous border somewhat narrow. The main veins bear long hairs. Costa lies widely separate on the fore border of the tegmen, with a large costal cell between it and the Sc, R, and M group. There is thus practically none of that massing of the main veins on the costal border so noticeable in other cicadas. The strong longitudinal grooving of the tegmen may counterbalance the general weakness due to this lack. This folding is very conspicuous, the costal cell and the anal furrow being especially depressed. Cu is peculiar (text-fig. 50); it forks early, and Cu 1 goes up to join M at the inner end of the anterior arculus, where the prominent boss on the surface of the tegmen makes the course of the veins difficult to follow. 1 A is extremely distant from Cu 2 and is strongly convex, lying on the brink of the deep anal furrow.

Text-figure 23.



Melampsalta cingulata. Male: KOH preparation to show junction of abdominal tergites and sternites.

III.-V., abdominal segments; *t.*, tergites; *s.*, sternites; 5–7, spiracles.

The cross-ridging of the tegmen (see later) is practically obsolete, probably owing to the coriaceous texture. The venation on the whole is strong, standing out in bold relief.

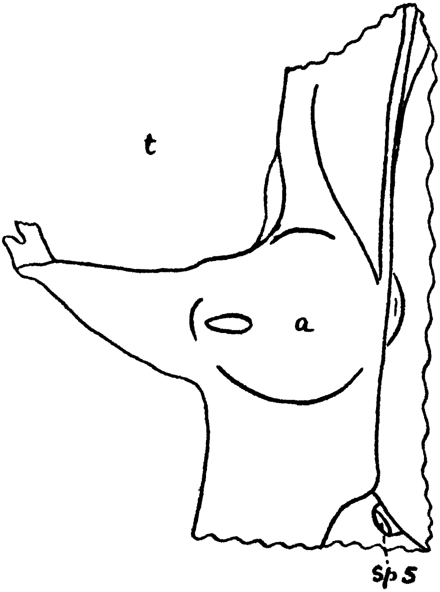
The hind wing of *Tettigarcta* (text-fig. 53) shows, as usual, more specialization than the tegmen. The hind wings of the Cicadidæ as a whole are mere appendages to the stronger and larger tegmina. Sc and R 2+3 are fused as far as the distal part of the wing-coupling apparatus (see later), where the common stem forks, apparently into Sc and R 2+3, so that a large additional cell, Sc, is formed. In conjunction with this the cross-vein *r* between R 2+3 and R 4+5 is carried very much nearer the apex of the wing. The cell Sc is squeezed out by vein coalescence in most other cicadas. A vestige is visible, almost hidden by the wing-fastener in the *Tibicen chloromera* figured (text-fig. 51).

The anal veins are distinctly three, arising from an apparently common base and spreading beautifully fanwise in a primitive fashion. Practically the whole surface of the hind wing shows innumerable microtrichia, which appear to be absent on the tegmen. The coriaceous border is as in the tegmen.

The axillary membrane in Cicadidæ is well developed and frequently coloured, when it affords a good taxonomic character. It contains the axillary sclerites, and is bounded posteriorly by the axillary cord (text-figs. 50 & 59, *ax.*).

The absence of R 1.—Muir (1923, p. 217) writes: "The absence of a distinct free R 1 in the adult tegmen is characteristic of most of the living Auchenorrhynchous Homoptera, but it is found in the Mesozoic Cicadid, *Mesogereon* Tillyard." We have seen that the R 1 trachea occurs in the nymphal wing of Cicadidæ, as also in that of Membracidæ. But I believe that the presence of R 1 in *Mesogereon* is only apparent—that it depends on an interpretation of *Mesogereon* tegmen different from that given here to the cicada tegmen. If we compare Tillyard's figure (1921, fig. 66) of *Mesogereon* tegminal venation, not with that of a typical modern cicada, but with that of *Tettigarcta* (fig. 50), which shows an intermediate condition,

Text-figure 24.

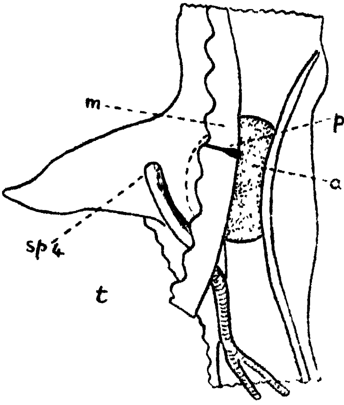


Melampsalta sericea. Male: external view of left auditory capsule. *t.*, position of tymbal; *a.*, auditory capsule; *sp.* 5, fifth spiracle.

R in both cases is seen to end in three branches meeting the margin of the tegmen or, rather, the coriaceous border. The condition in *Mesogereon* has necessarily been interpreted from adult structure only, and the first of these three branches has therefore naturally been called R 1, as indeed would probably the first of the three radial branches in *Tettigarcta* and also in more typical cicadas, did we not know from the nymphal tegmen of the latter that the true R 1 is lost in development. Therefore there is no proof that the first branch of R in the adult tegmen of *Mesogereon* is other than homologous with the first branch of R in modern cicadas, which we know from ontogeny is R 2.

The question of Costa.—I have followed in the foregoing the commonly-accepted Comstock-Needham interpretation of the anteriormost vein of the tegmen as C, since this view is based on, and seems to accord best with, the evidence from nymphal tracheation in Cicadidæ.

Text-figure 25.



As text-fig. 24, but viewed internally.

m., mirror (mostly cut away); *p.*, process to chordotonal organ; *ac.*, auditory capsule; *sp.* 4, trachea entering from fourth spiracle; *t.*, shows position of tymbal.

This vein, however, may not be true C. The recorded nymphal evidence in Auchenorrhyncha as a whole is conflicting, since in some forms the corresponding trachea seems to arise from the alar bridge, and in others from Sc, in which latter case it is apparently homologous with the humeral. Muir (1923, p. 216), in discussing the whole question, notes with reference to Fulgoroida:—

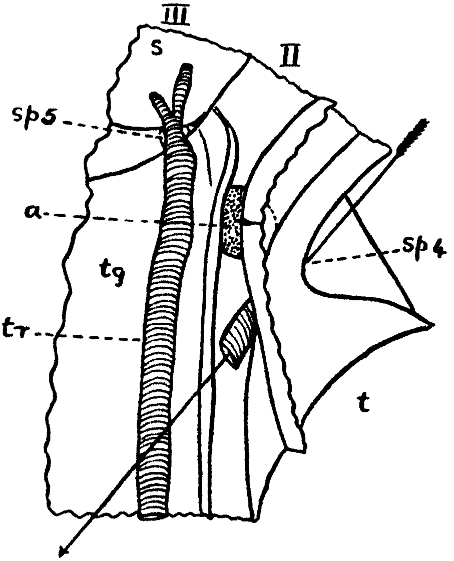
> "By calling this vein the costa we are faced by the fact that, in a large proportion of the fulgorids, the costa vein and costa margin do not coincide, but the vein lies considerably within the membrane, leaving a precostal cell or costal area. This is a condition recognized in no other order of insects."

Similarly, Tillyard[*] states:—

> "It seems, however, very unlikely that any true costal vein, distinct from the anterior border of the wing, was ever present in any Panorpoid type, seeing that *such a vein is absent from almost all known insect wings*." (Italics mine.)

Comstock has shown that R 1 is completely aborted (1918, p. 272). It would therefore seem that if our C is Sc and our R + Sc stem thus R alone, even then the vein we have called Sc, branching off, at the node, to the fore-border, would not be R 1, but rather a cross-vein between R and Sc. But here again we are led into difficulties, since, as we shall show below, Horváth is wrong in considering the vein on the fore-border, distal to the node, as a continuation of the anteriormost vein proximal to the node (his and our C). It tends to be continuous with the short vein, which leaves the R (or R + Sc) stem at the node, and which cannot therefore be a cross-vein.

Text-figure 26.



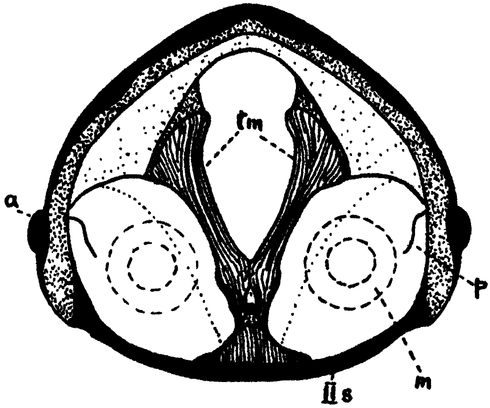
Fidicina semilata (Wk.). Internal view of male right auditory capsule. Arrow represents hair thrust into fourth spiracle, and through trachea which emerges from it; II., III., abdominal segments; *s.*, sternites; *tg.*, tergites; *t.*, position of tymbal; *a.*, auditory capsule; *sp.* 4, fourth spiracle; *sp.* 5, fifth spiracle; *tr.*, trachea (dorsal) arising from it and sending off a thinner ventral branch.

---

[*] Proc. Linn. Soc. New South Wales, xliv. p. 549 (1919).

Horváth believes Comstock and Needham incorrect in stating that C terminates at the node, its place on the anterior margin being taken by Sc. He claims that our Sc (text-fig. 48) is really a continuation of C past the node. Viewed dorsally in *Melampsalta muta* (text-fig. 52), C is seen distinctly to end at the node. Continuing its line is a piece of similar width and colour, but flat or even hollow, being the edge of the tegmen along the subcosta. Viewed ventrally, as Horváth suggests, this continuous portion anterior to Sc does look vein-like, but the convexity is merely the bottom of the grooved edge of the wing. Moreover, in the nymphal tegmen, the costal trachea is distinctly shorter than that of Sc, its termination being at a point corresponding with the node of the adult tegmen.

Text-figure 27.



Melampsalta sericea. Male: back view of mirrors (*m*) and tymbal-muscles (*tm.*, *p.*, process to chordotonal organ; *a.*, auditory capsule.

The costal area or precostal cell mentioned by Muir in the quotation above is well developed in some Cicadidæ, especially in some of the Platypleurinæ. Thus in *Yanga pulverea* and *Pycna madagascariensis* (text-fig. 57) there is a wide ampliation of the fore-border outside the costa. This precostal cell is as wide as (*Yanga*) or wider than (*Pycna*), the true costal cell. Such ampliation is an element in a general secondary platyptery considerably marked in these and related genera, and accompanied by the development of paranota.

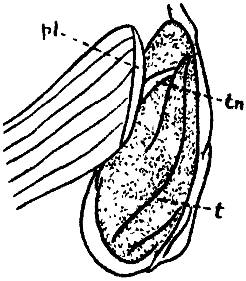
iii. *The Cross-ridging.*

A striking and peculiar feature of the tegmen of *Mesogereon* and of all Cicadidæ except *Tettigarcta* is the presence of numerous cross-ridges, especially visible in certain lights and interpreted by

Tillyard as archedictyal. In the Palæontinidæ there are apparently no signs of this cross-ridging, but the condition of the material is usually not such as to show such a character.

Forbes (W. T. M., 1922) saw this cross-ridging in an emerging cicada of undetermined species. For just a few minutes it was perfectly distinct. The arrangement was very definite; the narrow cells were filled with a series of simple evenly-spaced cross-veins, while in cells R, 1st M 2, and M they formed a double series of cells alternating with each other. On the coriaceous border beyond the ambient vein they were evenly spaced, the regular longitudinal veins each ending opposite the middle of a marginal cell. Towards the costa there were two veins opposite each definite cell, while opposite cells M 3 and M 4 there were three, and more posteriorly even four. The margin of the hind wing was similar, but the disc of the wing was not observed. In the cell 2 A, instead of cross-veins, there was a series of closely-spaced parallel longitudinal veins, which remained visible in the dried wing.

Text-figure 28.



Melampsalta sericea. Left tymbal from within to show attachment of muscle. *pl.*, terminal plate of tymbal-muscle; *tn.*, its tendon; *t.*, tymbal.

Forbes regarded these transient veins as "fugitive blood veins," and suggests they are relics of a net-veining such as occurs in the Neuroptera. He believes the different arrangement in the anal region especially suggestive, as it recalls the plaited portion of the wing in the Orthoptera, where there exist numerous parallel longitudinal veins.

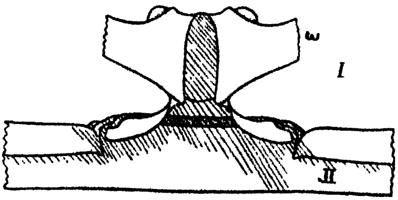
This agrees with Tillyard's original theory in 1916, when he saw in *Mesogereon*, on account of these cross-ridges, an intermediate stage between *Eugereon* and the Palæohemiptera. Though *Eugereon* is no longer considered Hemipterous, and the Palæohemiptera are disposed among recent groups, it still remains probable that this condition is a relic of the net-veining of a Palæodictyopteroid or Protorthopteroid-Palæodictyopteroid ancestor of the Hemiptera.

Goureau (1843, p. 204) remarked that the cicadas are exceptional in that the hind wings do not iridesce: Gadd (1908 *b*, p. 143) very rightly contradicts him, though admitting that the tegmina are certainly the more iridescent. The Russian author notices further that the iridescent wing-colours of older cicadas are predominantly yellowish, while those of younger ones are sky-blue.

iv. *The Nodal Line.*

This is a very remarkable structure, present to some degree in the tegmen of all Cicadidæ and especially marked in the very archaic *Tettigarcta* and in the probably primitive *Mogannia*, in which and in others the basal portion of the tegmen is thus separated as a more coriaceous and opaque part, at least superficially resembling a typically Heteropterous, *e.g.* Pentatomoid, condition. It is least developed in such a form as *Melampsalta* (text-fig. 58), but a point overlooked is that the breaks in the wing-veins where the nodal line crosses them are always complete, even in those which are most divergent from the *Tettigarcta*-like condition, Imhof has described the usual condition of the nodal line in 22 genera in very great detail (1905), recognizing 13 elements, and has enumerated the various kinds of joints and folds formed in veins and membrane by its passage. We show some of these joints enlarged in text-figs. 51 and 52. The nodal line begins on the costal margin at the distinct node, where the fore-border, *e.g.* in *Melampsalta cingulata*, is often bowed and, running between the termination of C and the basal part of Sc, cuts the Sc+R stem. It then curves in somewhat towards the wing-base and breaks M 2+3 and M 3+4 in succession, running then down Cu 1 *b* to the hind-margin (text-fig. 51). In the dominant modern cicadas, represented on the one hand by *Tibicen* and on the other by *Melampsalta*, the nodal line on the membrane between the veins is very indistinct, but is always visible if the insect be held at a certain angle. In those forms where the nodal line, as in *Mogannia*, divides a basal coriaceous, often brightly-coloured, corium from a distal transparent membrane,

Text-figure 29.



Magicicada septendecim. Male: inner view of portions of sternites I. and II. showing the wings (*w.*), which have been described as an abdominal furca.

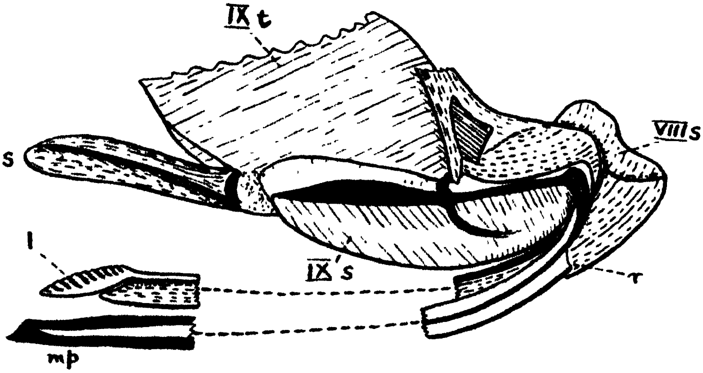
it is, of course, very distinct. In *Chonosia*, where such a demarcation is not present (text-fig. 49), the nodal line is nevertheless very well marked on the membrane. Finally, in *Tettigarcta* the nodal line is extremely conspicuous, crossing not only the veins, but forming on the intervening membrane a deep groove or fold, the lips of which appear as two fine parallel lines.

Imhof (*l. c.*) and Comstock (1918, fig.) both notice that the break in the veins where the nodal line crosses is not participated in by the tracheæ.

The nodal line is apparently not present in *Mesogereon*, and its absence, coupled with that of apical cells, makes me reluctant to place *Mesogereon* in the Cicadidæ as Muir would do.

In the Palæontinidæ, however, both it and the node are present to some degree, as evidenced by the published figures (Haase, Handlirsch, Oppenheim), and by the examples studied by me in the Museum of Comparative Zoology. One of the latter specimens shows a distinct break in the curvature of the costal border of tegmen, with an inwardly-curved transverse line of the same shape and relationships as the nodal line of cicadas, and apparently dividing off a more coriaceous basal portion.

Text-figure 30.



Melampsalta leptomera. Female: inner view of left half of pygophor, the anal segment boiled off.

VIII.-IX., abdominal segments; *s.*, sternite; *t.*, tergite; *r.*, cut edge of right median process; *l.*, left anterior process; *mp.*, middle piece, fused distally.

In the nymphs of all recent Cicadidæ examined the wing-pad itself shows a very distinct nodal line in the apical third, dividing off a very much thicker basal two-thirds. This condition appears strikingly Heteropterous.

So much for the facts. Their significance we believe with Horváth and Moulton to be great. Both these writers consider the nodal line homologous with that separating corium from membrane in the Heteroptera. We have discussed its possibly primitive character throughout the order in a later section devoted to phylogeny. Here we would give reasons for considering it a highly primitive character in the Cicadidæ:—

(1) It reaches its greatest development among adult cicadas in *Tettigarcta*, which in venation, head-structure, absence of sound-organs, and in other characters is the most primitive existing cicada.

(2) It shows an intermediate condition in such less primitive forms as *Chonosia* and other Tettigadinæ.

(3) It is least developed in those cicadas which are the most highly evolved in other directions, notably in development of the sound-organs and their accessories.

(4) It is highly developed and strikingly Heteropteroid in the nymphs of even the most modern cicadas, and in all of such that we have examined.

(5) It definitely occurs in the most cicada-like (Tillyard) all the pre-Cretaceous fossils—the Palæontinidæ.

(6) It is definitely present in *all* living cicadas known, and therefore represents a definite tendency of the cicada stem.

v. *The Wing-coupling Apparatus.*

The wing-coupling arrangements are simple in the extreme. A recurved flange on the dorsal surface of the median part of the costal border, hind-wing, hooks in a recurved flange on the ventral surface of the hind-border of the tegmen. The hind-wing flange is strengthened by the conjoined stem of $C+Sc+R\,2+3$ (text-fig. 51).

e. ABDOMEN AND ITS APPENDAGES.

α. General.

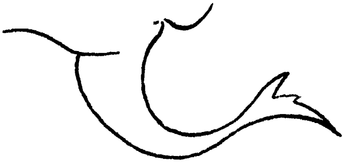
Ten distinct segments are recognizable in the cicada abdomen in both sexes, and, in addition, posterior to the tenth, are two successive parts of the anal "segment," which may perhaps be interpreted as segment XI. and a telson respectively, as Hansen (transl. 1902) suggests.

Segments I. and II. are modified extremely in the service of hearing and sound-production in the male, and of the former function alone in the female. They will be considered in greater detail when we come to describe the organs concerned. In both sexes, segments IX. and following are devoted largely to reproductive purposes, and will be described in connection with the external genitalia.

The tergites of the ordinary abdominal segments (text-figs. 11, 16) are greatly developed and strongly arched round the ventral surface. The sternites, bearing the 5th to 9th spiracles, are commensurately restricted.

There has been considerable discussion with regard to the lateral regions and as to the presence or absence of abdominal pleurites. Hansen (1902, p. 215) takes a somewhat broad band lying between tergite and sternite to be the pleuron. This consists of two parts—externally (dorsally) a conspicuous chitinous plate, which, except in swollen abdomens like that of *Cystosoma*, is separated from the tergite by a very narrow, thin, marginal membrane; and internally (ventrally) by a distinct, narrow, thin membrane between plate and sternite, again except in *Cystosoma*. Heymons (1899) gives valuable embryological evidence. He finds (p. 422) in the embryo very distinct and Heteropteroid *Tergitwülste*, which are passed on to the nymph and appear to be formed partly of tergite and partly of paratergite. They disappear in the adult, or rather become plates which are separated from the sternite by a suture, while laterally they reach the sharp body-edge (p. 424). These correspond to our under-arched part of the tergite, and are seen in text-fig. 11. Heymons (pp. 377, 417) denies entirely that special pleurites are present in any Hemipterous abdomen. He finds that in embryonic development each sternite consists of three plates, of which he calls the two lateral ones *parasternites*. These are represented in the adult cicadas at most by the "an das Stigma angrenzende Partie" of the ventral plate (pp. 377, 423). Neither paratergites nor parasternites are pleural in origin, though Verhoeff (1893) called them respectively "obere Pleuren" and "unteren Pleuren" in various other Hemiptera.

Text-figure 31.



Carineta formosa (Germ.). Male: external view of left lower pygophoral process (aborted genital style of Muir).

Vogel (1923), as we shall see in the description of sound and hearing-organs, recognizes quite a considerable development of the paratergites and parasternites—more than we can follow.

Doering (1922, pls. 59, 62, p. 558) shows in the abdomen of the Cercopid, *Lepyronia*, large and distinct "pleura" which seem to correspond with most of the lateral and ventral part of the tergite. It is possible she has used the term only in the topographical sense.

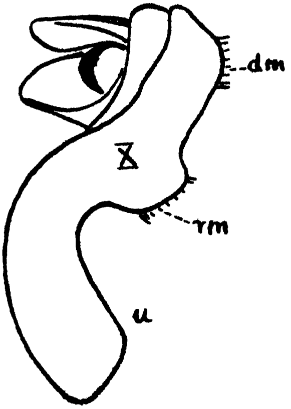
Berlese (1909) figures no abdominal pleural structures in any insect, and mentions (p. 255) as the acme of complexity Lacaze-Duthier's epimerite from the tergite and episternite from the sternite, evidently corresponding with Heymons's paratergite and parasternite.

Comstock (1925, p. 75) states that an abdominal segment consists typically of a tergum and a sternum united by lateral conjunctivæ. Sometimes there are one or two small sclerites in the lateral region which are probably reduced pleura.

Imms (1925, p. 41) states that the abdominal pleura are membranous and usually without differentiated sclerites.

We are therefore justified in interpreting the abdominal elements in cicada as a strongly-developed over-arched tergite meeting an entirely ventral sternite, which bears the spiracle.

Text-figure 32.



Tibicen chloromera Wk. Male: lateral view of entire anal segment.

X., tenth abdominal segment; *dm.*, right member of pair of dorsal muscles; *rm.*, right member of pair of ventral muscles; *u.*, uncus of American taxonomists.

It is true that there is an irregularly rectangular area at the side of each sternite, marked indistinctly by folds; but the spiracle is definitely in the main body of the sternite (text-figs. 11, 21). An internal view is seen in text-fig. 23.

The chief endoskeletal structures of the abdomen are the strong pegs found in the latero-ventral portions of the tergites and shown in text-fig. 23. The structure which gives support to the tymbal-muscles in the male, and is regarded by many as the furca of the first or of the second abdominal segment, we shall see later is not endoskeletal at all, but merely the modified ventral wall of the segment.

β. *Genitalia.*

Whatever be the number of abdominal segments admitted, we have seen that the IXth and succeeding ones in both sexes are

greatly modified either directly or indirectly for reproductive purposes. The VIIth and VIIIth are also somewhat altered. Although, as we shall see later, Aristotle described copulation, it remained for Malpighi (1687) and Réaumur (1740) to describe in any detail the organs concerned.

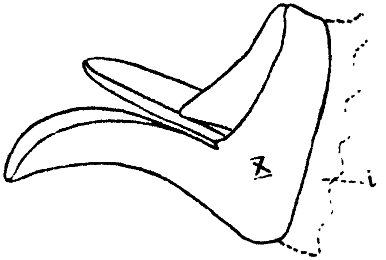
The descriptions which follow are based on *Melampsalta* spp.

i. *Male Genitalia.*

The male genitalia of Cicadidæ as emphasized by Kershaw and Muir (1922) are very distinct. The VIIth sternite is large and produced backward (text-fig. 35), its shape being a good taxonomic character. Whether the extension represents a development of the VIIth coxites is not known. The posterior border is often emarginate in the middle, and thus affords some slight evidence of primitive duality. The backward extension covers the base of the VIIIth sternite (hypandrium) as a crescentic free flap.

The VIIIth tergite is large and curved down latero-centrally so as almost to form a complete ring. The VIIIth sternite is large and boat-shaped and constitutes the hypandrium (text-fig. 35). There is some evidence—slight bilobation at the tip—that the fused coxites enter into the composition of the hypandrium. This condition is peculiar to the Cicadidæ. In all other Auchenorrhyncha these coxites are incorporated into the pygophor (IX.). In the trough of the hypandrium the pygophor lies at rest. Funkhouser (1917) figures a similar plate in Membracidæ, and considers it "apparently the sternum of the ninth segment." Newell (1918) would call it the IXth sternite in cicada, but there is no evidence for this and much to the contrary (text-fig. 35).

Text-figure 33.



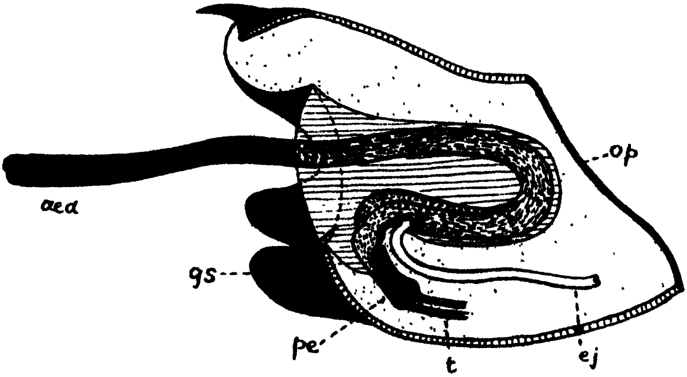
Melampsalta cingulata. KOH preparation of anal segment.
i., intersegmental membrane.

The pygophor is a strongly-chitinized more or less cylindrical case surrounding the termination of the gut and the genitalia. The whole of the dorsal and lateral portions are formed from the IXth tergite. The ventral surface is membranous and of uncertain origin. The lateral margin bears on each side a process, entirely non-articulate, which Muir and Kershaw homologize with the otherwise entirely lacking genital styles (text-figs. 31, 35). Singh-Pruthi does not agree with this homology (1925), and we think it rather doubtful. True genital styles are present in *Tettigarcta* (Muir, *in litt.*; Singh-Pruthi, 1925).

In repose no portion of the pygophor extends beyond the hypandrium terminally, but the tergal spine—a dorso-caudal projection of the IXth tergite—ends the dorsal line of the abdomen. This tergal spine, which is the "median dorsal spine" of Woodworth (1888), varies specifically, and is valuable in taxonomy *.

Distally the pygophor bears the anal segment or anal tube, made up chiefly of the Xth tergite. The Xth segment is produced ventrally into a more or less wide plate, extending in *Melampsalta cingulata* (text-fig. 35) directly caudad, but in *M. muta* and its relatives directly ventrad. Proximally to this again the edge of the anal segment bears two downwardly-directed, stout, curved, non-articulate hooks which I call copulatory claspers (text-fig. 35). These may be cerci—organs generally considered absent from the entire order, Hemiptera; they are appendages of the Xth segment, and thus in cicada the most distal, but they have lost all articulation. Crampton (1922, pl. 3. fig. 9) calls them "surgonopods (cerci?)." Newell labels them *cerci*, but notes that in no Hemiptera are these organs segmented (1918, p. 125). Berlese (1909, fig. 347) applies the term *cercus*

Text-figure 34.



Tibicen chloromera. Internal view of left half of male pygophor.

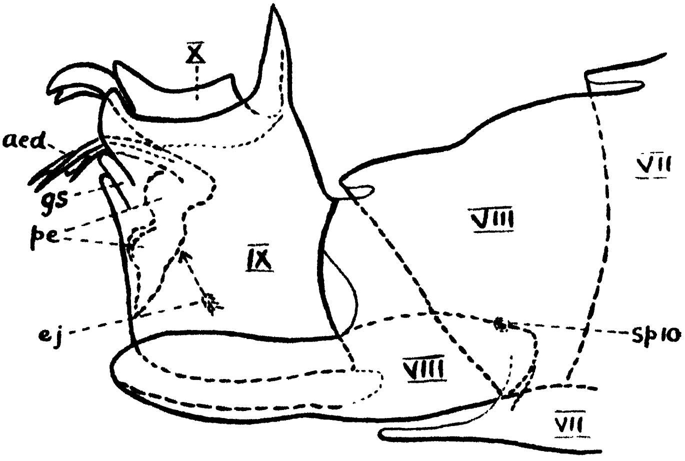
op., left half of basal opening of pygophor; *ej.*, ejaculatory duct; *pe.*, periandrial thickenings (*basal plates* of Singh-Pruthi); *gs.*, Muir's aborted genital style; *æd.*, ædeagus; *t.*, tendon for left member of pair of powerful muscles.

---

* The term *pygophor* is preferable to *pygofer*—a hybrid often encountered—and still more so to the plural form of the latter, frequently used. The dipterological term *hypopygium* is equivalent.

in the female to the epiproct, presently to be described, and in the male (fig. 399) to two smaller lateral pieces at their base. The copulatory hooks protect the ædeagus, which peeps out between them, and they thus take the place of the absent genital styles. In *Tibicen* and related genera the copulatory hooks are often fused in the middle line to form the *uncus* of American taxonomists (text-fig. 32, *u.*). This structure when single, as in *Tibicen chloromera*, shows a deep groove, proximally, in caudal view, marking the line of fusion. The base of each copulatory hook curves round and merely meets that of the opposite side, forming an aperture through which the ædeagus passes to the exterior. This is a much more specialized Xth segment than that of *Melampsalta*; yet the ædeagus is very much simpler—

Text-figure 35.



Melampsalta cingulata. KOH preparation, partially sectioned. VII.–X., abdominal segments: *sp.* 10, last spiracle (position only indicated). (For explanation of other lettering see text-fig. 34.)

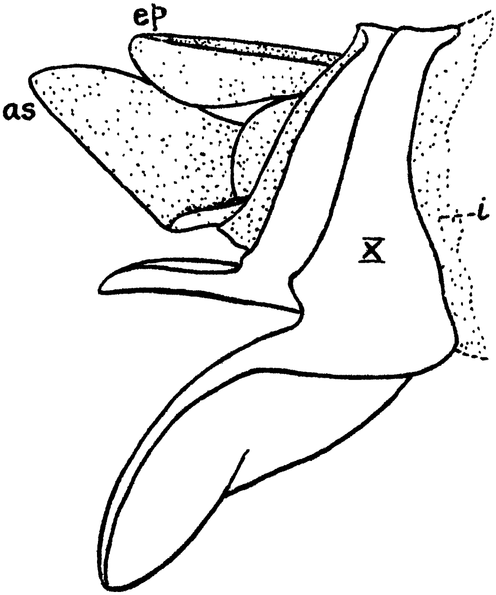
possibly by correlated reduction. In *Melampsalta cauta* the work of the uncus is performed by a strongly-curved plate which looks very much like one, but is distal to the true copulatory hooks which lie beneath it, and is thus homologous with the directly caudal extension of segment X. already described in *M cingulata* (text-fig. 35). Both this and the true copulatory hooks are shown distinctly in lateral view in text-figs. 33 and 36 of *cingulata* and of *sericea* respectively. The condition in the latter suggests that the second projection may possibly pertain to an XIth segment. The modification of the Xth segment occurs in no other Hemiptera (Singh-Pruthi).

Beyond the anus and the Xth segment is a dorsal lamina or epiproct (text-fig. 36, *ep.*) and a ventral one or *anal style* (*as.*).

The former is the telson of Doering (1922) in the Cercopidæ. At the base of these on each side is a rounded, sometimes shining black plate which Berlese (1909, fig. 399) labels *cercus*, but which is more conceivably a podical plate from which the cercus has been lost.

Ædeagus.—In *Melampsalta* this consists of a stout, basal, bilobate bulb, the *periandrium*, and three long distal processes surrounding and more or less parallel to the penis itself. Muir and Kershaw (1922, p. 205) call the distal portion of the ædeagus the *penis*, but it would seem better to restrict the term ædeagus to the actual sheath. Of the three arms of the ædeagus, two are lateral and the third median and bearing distally the orifice of the penis.

Text-figure 36.

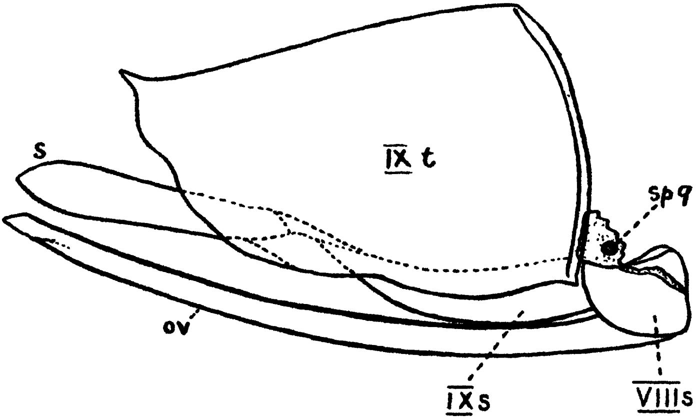


Melampsalta sericea. Male: anal segment complete, soft parts stippled. *ep.*, epiproct; *as.*, anal style; *i.*, intersegmental membrane.

The periandrium arises as a thickening in the body-wall between the IXth and Xth segments. These thickenings (*ipofallo* of Berlese) are called *basal plates* by Singh-Pruthi (1925, p. 136), and considered of very great morphological significance. He would homologize them with certain distinct sclerites near the bases of the ædeagus and the genital styles in such other Homoptera as Cicadellidæ. This homology would seem to be entirely fanciful. Singh-Pruthi states that "basal plates" are present in Cicadinæ Dist., Gæaniinæ Dist., and some Tibicininæ, but are absent in the rest of the latter. In such forms as *Tibicen* the thickenings of the periandrium are certainly very strongly developed (text-fig. 34, *pe.*), but it would appear that no hard-and-fast line can be drawn. On this basis Singh-Pruthi considers that the cicadas of the subfamily Platypleurinæ (Cicadinæ Dist.), usually believed on other counts to be the most highly evolved of the family, exhibit the most primitive conditions.

In spite of its frequent complexity the Cicadid ædeagus may be considered relatively primitive. It shows little of that invagination of the distal into the proximal portion characteristic of many other Hemiptera—*e. g.* Fulgoroidea and Heteroptera. It is, however, true that Apgar (1887) has described quite a complicated endosome in the ædeagus of *Magicidada septendecim*, while in most cicadas the whole ædeagus occupies a somewhat internal position, brought about by invagination of the ventral membrane of the pygophor and of the intersegmental membrane between that and segment X.

Text-figure 37.



Melampsalta leptomera. Lateral view of ovipositor and related parts; anal tube boiled off.

s., ovipositor sheaths; *ov.*, ovipositor.

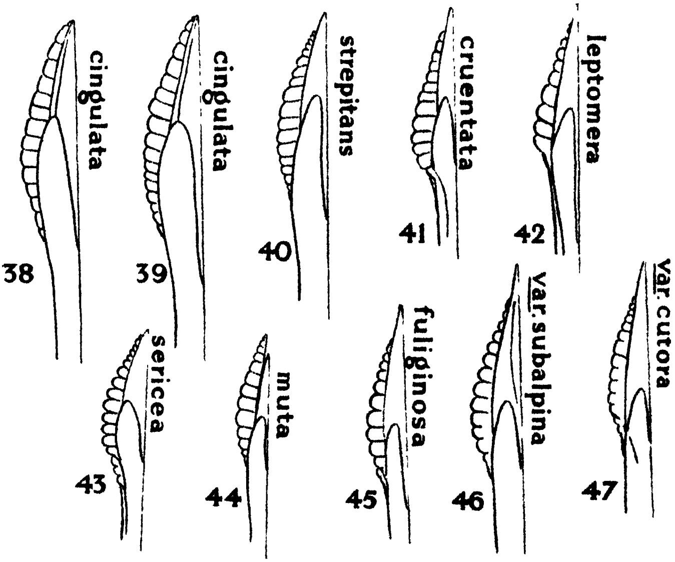
The chief workers on the genitalia of male Auchenorrhyncha, and incidentally of Cicadidæ, have been Malpighi (1687), Réaumur (1740), Dufour (1833), Newell, Heymons, Kershaw and Muir (1922), Muir (many papers), Lawson, Singh-Pruthi (1924, 1925), Doering (1922).

ii. *The Female Genitalia.*

The female genitalia consist essentially of three pairs of appendages, frequently known as *valves*. These make up the ovipositor and its sheaths. The central or inner pair is fused for the greater part of its length, forming distally a single solid piece (text-fig. 30, *mp.*) with sharp strongly-chitinized apex. The pygophor is not unlike that of the male in shape (text-fig. 37, IX. *t.*), with a longer and more tubular anal segment which lacks the armature of that of the male, but is otherwise essentially similar.

The central piece formed by fusion of the inner pair acts as guide-piece for the outer or proximal pair which partially encloses it (text-fig. 30, *l.*). The three pieces are welded into a functionally single weapon by means of at least three pairs of interlocking grooves and ridges, well shown by Marlatt in cross-section (1907, fig. 37). Such interlocking, while effectually preventing lateral movement of individual pieces, allows and indeed facilitates longitudinal sliding of the ventral or outer pair on the middle piece, the tip of which is sharp and hard. The apices of the ventral or lateral pieces (text-fig. 30, *l.*) beyond the tip of their infolded portion clasping the middle piece are likewise blackly, heavily chitinized and furnished with a number of oblique cutting-edges. These are the effective instruments of perforation. Lawson was the first to figure these in detail for a

Text-figures 38–47.



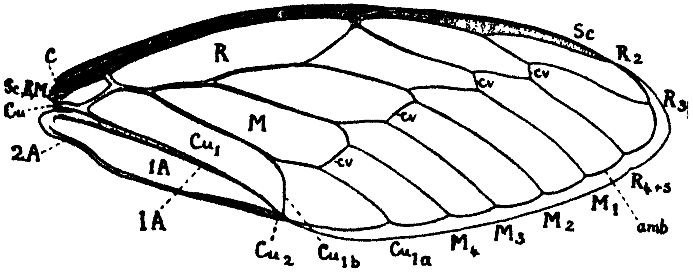
Ventral view of ovipositor tip, left half, of species of *Melampsalta*: *cingulata* (2 specimens), *strepitans* (Kirk.), *cruentata* (F.), *leptomera*, *sericea*, *muta*, *fuliginosa* Myers, and *muta* vars. *subalpina* (Huds.) and *cutora* (Wk.).

number of species (1920, pls. 24, 25) and to claim that they are of considerable value in taxonomy. Nothing is more needed in cicada systematics to-day than some new character independent of male characters, but our experiences in *Melampsalta* (text-figs. 38-47) do not lead us to hope for very much from these as characters for specific separation.

While the proximal portion of the whole ovipositor is protected laterally if not ventrally by the pygophor, its distal part is ensheathed by the third pair of appendages, which are less strongly chitinized, apically rounded, and usually hairy (text-figs. 30, 37, *s.*).

Attachments of Ovipositor.—The lateral pieces arise from the VIIIth sternum (text-fig. 37, VIII. *s.*), which is represented by two triangular sclerites largely hidden by the VIIth, which, as shown in text-fig. 11, abuts largely on the base of the ovipositor. The dorsal basal angle (*outer b. a.* of Muir and Kershaw, 1922, in Cercopidæ) of the lateral pieces is joined to the posterior basal angle of the IXth tergite as shown in text-fig. 30. The IXth sternum, in so far as it is chitinized, consists of a large, somewhat elongate, boat-shaped sclerite or plate situated on each side of the mid-ventral line and homologized with the orthopteroid valvifer. Proximally this gives rise to the middle piece, formed by the fusion of the inner pair of appendages, which are perfectly separate for some distance from their origin. Distally the IXth sternal sclerites are continued by a membranous area, shown stippled in text-fig. 30, into the two hairy appendages (*s.*) forming the ovipositor sheath. Berlese (1909, pp. 302, 303, fig. 347) would homologize the latter with the prostili of Orthoptera.

Text-figure 48.



Melampsalta muta. Right tegmen.
amb., ambient vein.

(N.B.—Venation for text-figures 48-59. The usual abbreviations of the Comstock-Needham notation employed.)

The various names applied in taxonomic and morphological literature to the three pairs of gonapophyses comprised in the ovipositor and its sheaths are so confusing that we are impelled to submit a table of them.

$g.^1$=saw-valves (text-fig. 30, *l.*), ventral valves (Tillyard, Doering), anterior, outer, or ventral processes (Muir and Kershaw).

$g.^2$=middle piece (text-fig. 30, *mp.*), inner valves (Tillyard), median processes (Muir and Kershaw), dorsal valves (Doering).

$g.^3$=sheaths (text-fig. 30, *s.*), dorsal valves (Tillyard), posterior processes (Muir and Kershaw), lateral valves (Doering).

The first writer to concern himself with the structure of the ovipositor was Aristotle, who merely notes:—

> "pariunt [Cicadæ] in aruis cessantibus, excavantes asperitate præacuta, quam parte habent posteriore. . . ." *Hist. anim.*, Gaza, lib. v. cap. 30.

Malpighi (1687) gives a ventral view of the ovipositor (ii. p. 38, tab. xi. f. 2) showing some detail, and then proceeds to describe it as the male genitalia, thus:—

> "In *Cicadis* etiam fœminis, eadem pudendi conformatio imum ventris occupat: in his penis A binis constat assibus, quorum extremitas, pluribus eminentiis aspera, glandem B constituit; custoditur autem vagina C, quæ et ipsa in binas aperitur partes non longe ab ano D."

Yet on an earlier page (i. p. 129, fig. 73) he writes:—

> "In Cicadis (73) insignis magnitudinis terebra extat, quam olim pro pene, ita deceptus, delineavi. Hujus structora miram Naturæ sagacitatem patefacit."

Then follows a good and detailed description of the ovipositor; but a passage on p. 131 still leaves it doubtful whether he really knew the male genitalia.

These latter were considered with admirable detail and figured with much clearness by Réaumur (1740), whose description of the ovipositor, more masterly than that of his great predecessor, became the reference account for subsequent entomologists almost to the present day.

Later workers on the structure and homology of the female genitalia of Auchenorrhyncha in general or of Cicadidæ in particular are Doyère (1837*a*), Hyatt (1896), and Heymons, Verhoeff, Kershaw and Muir (1922).

iii. *Homologies of the Genitalia.*

Kershaw and Muir (1922) would homologize the genital appendages in the two sexes. They find the more general condition in Homoptera to be as follows. (For convenience in reference we have collated the synonymy):—

$g.^1$=anterior gonapophyses =appendages of VIII.
=hypovalvæ (Crampton).
=genital plate (Kershaw & Muir). } Male.
=subgenital plate (Singh-Pruthi).
=outer processes of ovipositor.

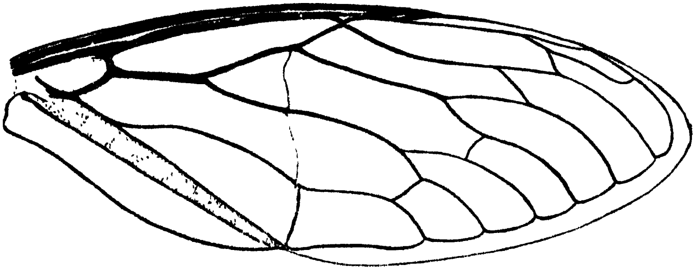
$g.^2$=median gonapophyses =appendages of IX.
=ædeagus of male.
=middle piece of ovipositor.

$g.^3$=posterior gonapophyses=gonocoxites of IX. (Tillyard).
=genital styles (K. & Muir). } Male.
=parameres (Singh-Pruthi).
=ovipositor sheaths.

In the cicadid female all three pairs are well represented; in the male $g.^1$ are apparently lacking, though perhaps fused in the hypandrium, while $g.^3$ are practically aborted save in *Tettigarcta*.

Several writers, notably Doering (1922) and Singh-Pruthi, have questioned this homology on morphological and embryological grounds, and Muir (1925) has reviewed the evidence anew.

Text-figure 49.



Chonosia crassipennis (Wk.). Tegmen of aberrant specimen, with abnormal Cu 1.

Tillyard, in his new general work (1926), agrees that a complete homology exists between the two sexes.

While most writers agree that the posterior two pairs of gonapophyses—the ædeagus and genital styles of the male and the inner processes and outer sheaths of the female—are homologous in the two sexes, Kershaw & Muir and Tillyard would appear to be alone in considering the anterior pair so also. The former have brought forward very convincing evidence for their view. As, however, the question can be settled only by renewed embryological work and by comparative studies not only in Hemiptera but in other orders, it is outside the scope of this paper and need concern us no further here.

(2) INTERNAL ANATOMY.

Our alcohol material being scanty, we have been compelled to use most of it for the elucidation of the digestive system, and, with reference to the other organs, to make what incidental observations we could and collate previous references.

a. Nervous System.

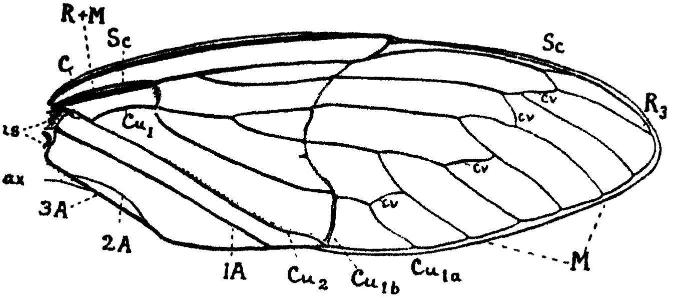
α. General.

The chief writers to concern themselves with the nervous system and sense-organs of Cicadidæ, either especially or incidentally, were Meckel (1818) and Dufour (1833), who laid the foundation of so many branches of Hemipterous anatomy, Brandt (1878), Rossi (1879–1880), Binet (1894), Berlese (1909), Swinton (1877 *b*, 1879–1880), and Vogel (1922, 1923); Will (1840), Grenacher (1879).

Meckel described in *Tibicen plebeia* the brain and 4 "Knoten," the last larger.

Dufour (pp. 264–266, separate pagination) described in *Cicada orni* L. a cephalic ganglion and two thoracic ganglia. He noticed that the former was produced by a fusion of two hemispheroid lobes, the fissure separating which was only superficial.

Text-figure 50.



Tettigarcta crinita. Tegmen.

as., axillary sclerites; *ax.*, axillary cord.

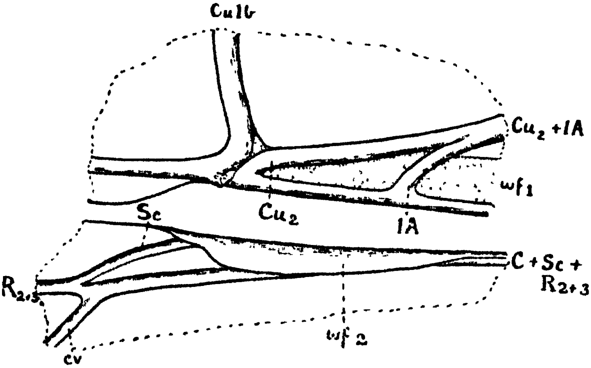
(N.B.—Text-figs. 48–52 are of different magnifications.)

The anterior part gives rise to an optic nerve on each side. This nerve, pyramidal or shortly, thickly club-shaped, embraces the ocular bulb. Anteriorly arises a trifid nerve of which the three branches go to the ocelli. The œsophageal ring gives rise to a pair of nerves for the muscles moving the head. The thoracic ganglia, far from being separate and distinct as in *Nepa*, are nearly fused into one, as in the "Geocorises." With difficulty one traces the light demarcation of an interior ganglion. The ensemble of the two ganglia forms an oblong body, deeply situated beneath the muscle-masses which fill the lower wall of the thorax. The anterior ganglion gives rise to four pairs of principal nerves, and the posterior to six. The two nerve-cords, towards their origin, are contiguous as if adherent, but in the abdominal cavity they separate before finally dividing.

Such in brief is Dufour's century-old description, and it is surprising how little from the gross anatomical viewpoint can be added thereto to-day. Text-fig. 70 shows certain rather striking differences in *Melampsalta sericea* from the condition described by Dufour in *Cicada orni*. If these be confirmed they would go to show that there is considerable diversity in the family, and that *Melampsalta* is considerably less specialized than *orni* in the development of the nervous system. Instead of the two thoracic ganglionic masses distinguished with difficulty in *orni*, there are in *sericea* three, the foremost of which is quite distinct. Dufour makes no mention of a sub-œsophageal ganglion, which he probably confused with the brain itself.

Remarkably little is known about the general nervous system of any Hemiptera, and there is but scanty material for comparison. It would appear, however, that the Cicadidæ are considerably specialized so far as the nervous system is concerned, although less so in some respects than the Cicadellidæ (Jassoidea), in which, as for instance in *Dræculacephala*, Cogan (1916, pl. 22. fig. 32) shows the whole central ganglionic system as practically one elongate mass with a small aperture for the œsophagus.

Text-figure 51.



Tibicen chloromera. Wing-coupling apparatus—part of hind-border of tegmen and fore-border of hind wing, in dorsal view.

wf. 1, downfold of tegmen (viewed through membrane of wing); *wf.* 2, upfold of hind wing.

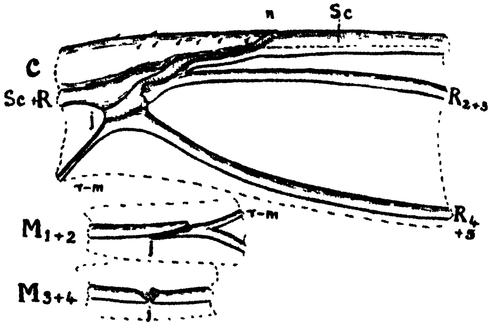
Berlese finds that in some Coccids and Heteroptera the sub-œsophageal ganglion is fused with the *thoracic* mass.

Binet (1894) has supplied perhaps the most thorough study of the subintestinal nervous system in cicadas (*Cicada orni*). He remarks first of all (p. 486):—

"parmi tous les Insectes que nous avons étudiés, nous avons trouvé les cellules nerveuses les plus considerables chez la cigale; on trouve dans la région abdominale des centres nerveux de cet Insecte deux cellules géantes mesurant 150 μ suivant leur plus grand diamètre."

But Binet's greatest discovery (pp. 542, 543) concerns the abdominal ganglia, which, though fused with the last thoracic mass, are nevertheless distinguished in sections by the absence of crural lobes, correlated with the absence of legs in the corresponding segments. The first abdominal ganglion differs from the succeeding ones in possessing a swelling of the dorsal lobe. This swelling is formed by two very distinct lobes, which are superadded to the dorsal lobe of the ganglion. Each of them occupies the externo-superior position, and they are separated by a deep indentation where the great ganglionic cells accumulate. The two lobes are situated in front of a ganglionic cell of exceptional size, which lies at the level where the crural nerves enter the central nervous system. A longitudinal section shows that each of the new lobes is situated just behind the corresponding metathoracic crural lobe. The *vocal lobes*, as Binet calls them, are intimately united with the dorsal lobe of the ganglion, which is essentially motor. They have no adherence to the ventral lobe, from which they remain distant for all their extent. Thus they differ from the crural lobes, which, situated laterally, in relation at once with the sensory (ventral) and motor (dorsal) lobe, are both sensory and motor. The vocal lobe "paraît être uniquement doué de fonctions motrices."

Text-figure 52.

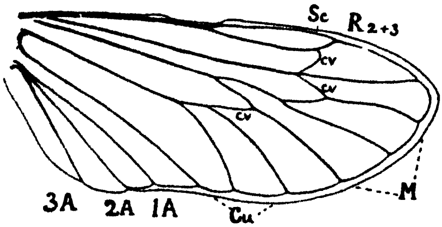


Melampsalta muta. Part of right tegmen, viewed dorsally.
n., node; *j.*, joints or breaks in the veins.

It will be interesting to study the relations of the auditory nerve, discovered since Binet's time, with the abdominal ganglion in question. Vogel (1923) describes it as branching from the abdominal strand, apparently in the IInd segment. Our material at present fails to settle this point.

We have examined the gross anatomy of the nervous system in unsuitably-preserved material of *Melampsalta muta*, *M. sericea*, and *Carineta formosa*. The brain is esconced on the second swelling of the digestive canal, just behind the dorsal dilator muscles of this organ. It is considerably wider than long (text-fig. 70, *b.*). The optic nerves are huge and long, and *corpora pedunculata* lacking. Berlese notices that the protocerebral lobes are small and the others still smaller. The ocellar nerves are as described by Dufour—their branching from the common stem does not occur until just below the ocelli themselves. Berlese figures the brain of *Tibicen plebeia* (text-fig. 697), a section of the procerebral mass in the same insect (text-fig. 694), and also a section of its whole brain (Tav. VI, ii.).

Text-figure 53.



Tettigarcta crinita. Right hind wing.

The œsophageal connectives (text-fig. 70, *c.*) are stout and rather long—in *Melampsalta* less so than in *plebeia*, as figured by Berlese. The subœsophageal ganglion is rounded, joined by long, stout, well-separated cords to the first thoracic ganglionic mass, which lies largely in the prothorax. This has two short, very stout connectives to the second thoracic mass, which is much longer than broad and shows signs of two-fold origin. It lies wholly within the mesothorax and, in fact, does not reach the mesophragma. Posteriorly it passes into a superficially single cord which splits into two as it enters the abdomen. From the standpoint of gross anatomy the abdominal ganglia fused in the second mass are not to be distinguished.

The sympathetic nervous system has not been studied in Cicadidæ nor related families.

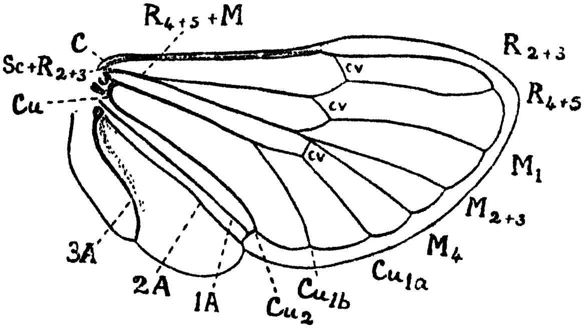
β. *Eyes and Ocelli.*

The compound eyes have been studied in *Cicada orni* L. by Will (1840) and in *Cicada grossa* (?) by Grenacher (1879). According to the former, each eye in *orni* has 11,600 ommatidia (p. 11). Grenacher (p. 96) finds the eyes are of the eucone type, *i. e.*, each visual element contains a true crystalline cone, in front of which are the nuclei of the cone-cells. The retinula is formed from eight distinct elements, and the crystalline cones are very well developed.

The compound eyes in Grenacher's opinion approximate most closely to the Hymenopterous type and differ "sehr beträchlich" from the Heteropterous—a fact which need not occasion surprise when one considers how largely Cicadidæ appear to depend upon their eyes.

Their habit of dodging like a squirrel behind a branch, keeping it ever between themselves and the observer, is very amusing, and is shared also by certain Heteroptera, notably mirids. That the compound eyes are the chief organs involved is suggested by the absence of ocelli in Miridæ.

Text-figure 54.



Melampsalta muta. Right hind wing.

The ocelli are three in number and markedly red in colour. Berlese (1909, p. 672, fig. 840) has studied in some detail those of *Tibicen plebeia*, while Link in the same year (pp. 354–356, text-fig. O, Taf. 24. fig. 27) gives a more thorough-going account in "*Cicada concinna* L." (= ? *Cicadatra atra* (Oliv.). The most striking feature is the presence of pigment-cells between the sense-cells—a characteristic of Auchenorrhyncha. Link shows that these red pigment-cells are derived from the corneagen layer. Berlese (1909, p. 672), however, disagrees. The pigment is in the form of red granules, filling the cells.

Link erroneously considered the "Gattung *Cicada*" as the only one in the Homoptera furnished with three ocelli.

We have seen that the ocellar nerves are bound in a common stem to near the ocelli. Link goes further and finds that the branch then proceeding to the median ocellus is really double, whence he speculates whether this condition is secondary, or denotes fusion from an original pair. Hymenoptera and

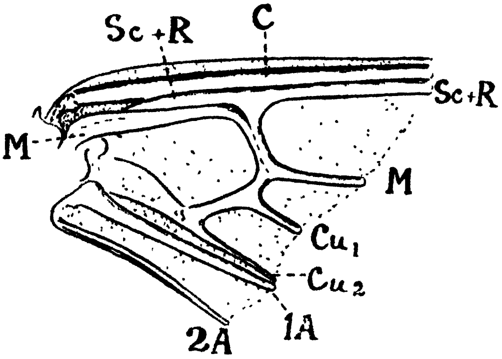
Odonata—notably insects with well-developed visual powers—share this arrangement with the cicadas.

Link repeats the well-known hypotheses that the function of the ocelli may be connected with the need for sudden movements—since they are well developed in most jumping insects—or with orientation, as suggested by their position.

In an insect like a cicada, with the head and prothorax almost immovably fixed to the rest of the body, the ocelli would certainly seem to complete the visual equipment so far as direction is concerned. The field of the great compound eyes is largely lateral; the paired ocelli look directly upward, while the median one is often on an eminence which directs it forward.

Whatever be the respective functions of this rather complicated visual apparatus, no one who has collected cicadas will question the ability of the insects to use it very effectively.

Text-figure 55.



Tibicen chloromera. Base of right tegmen.

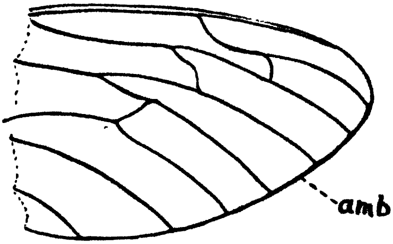
γ. *Auditory Organs.*

The supposed absence of auditory organs in the Cicadidæ was long one of the chief arguments against any sexual significance in the song. To Swinton (1877 *b*, 1879, 1880) must be given the credit for discovering an organ to fill this lack. Unfortunately Swinton wrote in such an involved style, euphuistic, highly allusive, and abounding in long irrelevant discussions, that he effectually disguised the solid scientific contribution often contained in his writings. In reading him one had always the impression of vapourising dilettantism; one met never without surprise every additional citation indicating that he knew thoroughly the literature of his subject. One does not expect an epoch-making discovery among the amiable ramblings of an undated volume with such a title as 'Insect Variety: its propagation and distribution.'

It is true that Swinton reported very briefly his investigations also in a scientific periodical (1879); but, for all that, they were completely ignored by all subsequent workers until practically the present day. The masterly and detailed description of cicada auditory organs by Vogel in 1923 involved their discovery anew, and it was not until Vogel's work was well on the way to completion that he found Swinton's long previous account.

The first detailed descriptions of cicada sound-producing organs had made known the mirror—an extremely thin and delicate, beautifully iridescent membrane closing the cavity of the sound-apparatus posteriorly. In spite of at least some experiments to indicate the contrary, almost every observer since and including Réaumur has assumed that the mirrors act as resonators. This will be found in every modern account of cicada sound-organs. Swinton's contribution consisted in his recognition of the mirror as the tympanum of an auditory organ.

Text-figure 56.



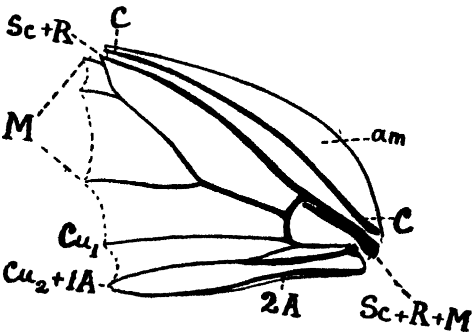
Lembeja fatiloqua (Stål). Apical half of right tegmen. *amb.*, ambient vein.

Swinton was purely an amateur, and could not have elucidated the microscopic structure of the chordontal organ itself, even had he seen it. He described, however, the auditory nerve, the thickened line on the tympanum, the spatulate process at its lateral extremity, and the external appearance of the auditory capsule.

To Vogel alone we owe a complete account of this remarkable organ and its accessory structures. The mirror is seen at M (text-figs. 11, 17, 18, 19, 20, 27). It is an extremely fine skin, according to Vogel, only 5 μ thick in the middle, in two species of *Melampsalta* studied by him. As to its origin, that is so wrapped up with the development of the sound-organs that we must consider them together when the latter are described. For the present we content ourselves with a brief account of the sound-organ as it occurs. In the lateral part of each tympanum is a dark thickened line (text-fig. 19, *p.*) which leads centrewards but never reaches the middle. From the broadened lateral end of the thickening arises a spatulate chitinous process, running obliquely into the auditory capsule, where it serves as an attachment surface for the sense-organ.

The auditory capsule is a more or less hemispherical swelling (*a.*) on the ventro-lateral portion of the IInd abdominal tergite (paratergite, Vogel). The lumen contains hæmolymph and blood corpuscles, the last often accumulated in the angles. Where the capsule joins the body-wall, there are outgrowths forming surrounding chitinous rings and making the capsule larger and more nearly spherical (text-figs. 25, 26). Only on the middle of the inner surface of the capsule there remains a larger oval opening, which is covered by thin membrane (according to Vogel, the wall of the tracheal sac, as he names our mesenteric sac). Vogel calls this opening the *fenestra ovalis*, from analogy with the vertebrate ear. On the ventral side the capsule communicates with the abdominal cavity by a slit overlaid by the mesenteric sac. This slit leads into one of the grooves formed by the sternum of the IInd abdominal segment (text-fig. 26).

Text-figure 57.



Pycna madagascariensis (Dist.). Basal part of left tegmen.

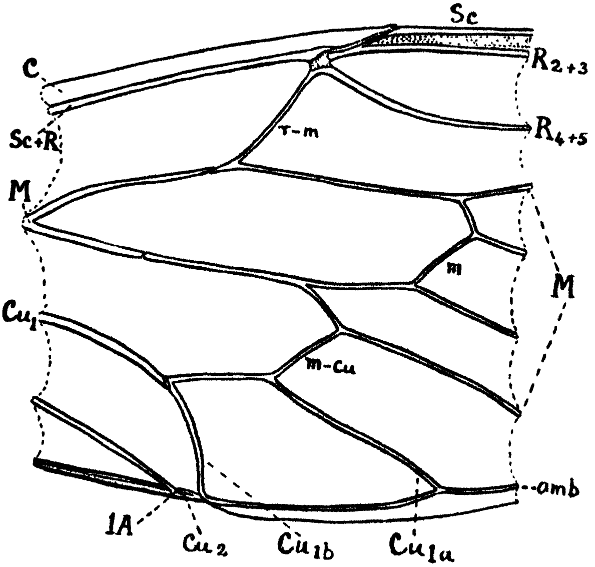
am., ampliate precostal area.

The actual sense-organ itself is stretched in the cavity of the auditory capsule, between two spring-like chitinous pieces. One is the spatulate process from the typanum, while the other is an invagination of the outer wall of the capsule, where it appears as a slit in external view (text-figs. 16, 17, 24). The spatulate process lies in the same plane as the tympanum, from which it arises.

The sense-organ shows all the structure of a chordotonal organ in so far as its sense-cells terminate in the usual rod-like bodies or scolopales, and are stretched by means of fibrillar differentiated hypoderm cells between two points of the cuticle. It is distinguished from all hitherto-described chordotonal organs by the enormous number of sense-cells or scolopophores. Schwabe found upwards of a 100 in the tympanal sense-organs of Locustids and Gryllids; the cicada, *Melampsalta coriaria*, studied by Vogel has about 1500. But the most important distinction shown in cicadas is that the proximal fastening point is differentiated into a tympanum whose swinging is registered by the sense apparatus. Usually it is the distal one which is thus modified.

Vogel speculates as to whether the scolopophores, in their tremendous numbers, are capable of sound-analysis in a manner analogous to that of the fibres of Corti. In *Melampsalta coriaria* they vary in length from ·2–·31 mm., as compared with ·04–·5 mm. in Man (Helmholtz). He decides that there would probably be only a small range. If it were demonstrated it would go far to explain the great effect of certain sounds on cicadas and their indifference to others, as in Fabre's classical experiment with the festal cannon, which the cicadas ignored entirely.

Text-figure 58.



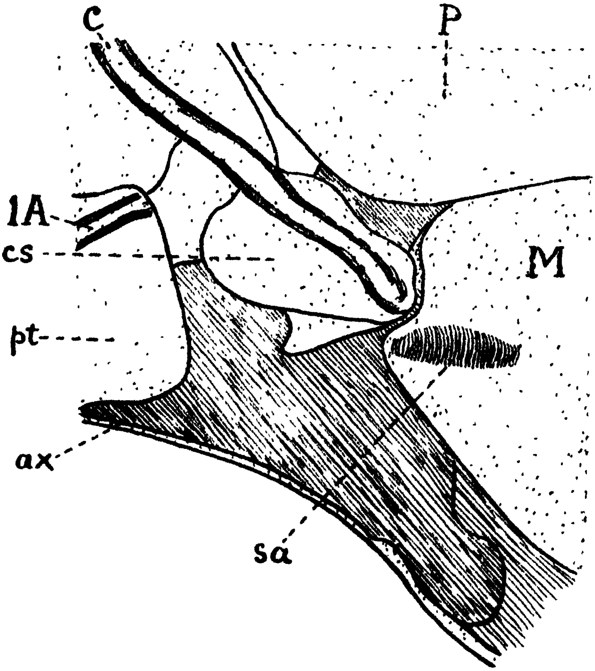
Melampsalta muta. Portion of right tegmen to show chief elements of nodal line.

For the histology of the sense-organ itself we must refer to Vogel's very able paper (1923). There remain several accessory structures to mention.

The first is a simple dorso-ventral muscle which acts as a *tensor tympani*.

The second is Vogel's great *tracheal sac*, which he describes as abutting on the inner side of the sense-organ and of the tympanum and acting as a pressure-equaliser, maintaining air-pressure equilibrium on both sides of the tympanum with which he claims that its wall is fused. This "tracheal" sac is apparently the mesenteric sac which we hope to deal with in a later section. It has been the subject of endless controversy, some contending that it is part of the digestive tract and others that it is part of the tracheal system. We believe that we have confirmed the work of those who regard it as mesenteric in origin, and we have certainly found no trace of a connection with the tracheal

Text-figure 59.



Chonosia crassipennis. Part of notum and base of tegmen of male to show the stridulatory organ.

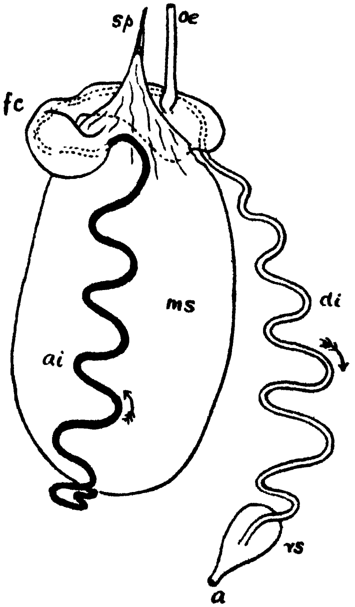
sa., stridulating area; *p.*, pronotum; *m.*, mesonotum; *c.*, costa; *cs.*, costal sclerite; *pt.*, posterior tuberosity of tegmen; *ax.*, axillary cord of tegmen.

system, nor do we believe that its wall fuses with the auditory tympanum or mirror. The whole evidence is discussed in the section on the alimentary system.

With regard to the auditory nerve, Swinton (1879, p. 81) traced it from a thoracic ganglionic mass to the abdomen and round the tymbal muscle, after which his description becomes obscure. The "acoustic" nerve is said then to form a "ganglion" that "enters a groove."

According to Vogel the auditory nerve arises in the IInd abdominal segment from the two great ventral nerve-strands, and rises, running parallel with the body-wall, in a chitinous groove dorsally to the sense-organ, where its fibres run one into the base of each sense-cell. In my poorly-preserved material I found a distinct nerve emerging on each side of the last thoracic ganglionic mass near the end, and running parallel to the abdominal cord. I followed it nearly to a chitinous ridge leading up to the auditory capsule, and suspect that it is the auditory nerve. It seems very improbable that it should arise from the abdominal strands, as Vogel seems to state.

Text-figure 60.



Carineta formosa. Ventral view of alimentary system, entirely schematic.

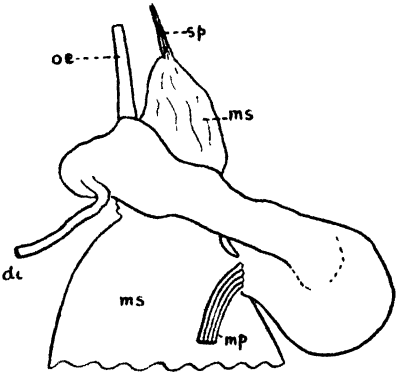
oe., œsophagus; *sp.*, suspensory ligament of mesenteric sac; *fc.*, filter-chamber (stomach); *ai.*, ascending intestine (mid); *di.*, descending intestine (hind); *ms.*, mesenteric sac; *rs.*, muscular rectal sac; *a.*, anus.

In the primitive *Tettigarcta*, which lacks all trace of sound-organs, I have been unable to find, in the two females available, any signs of an auditory capsule or of a tympanum. But the evidence is not conclusive, since these specimens were rather badly attacked by ants before they came into my possession, and were especially damaged on the basal abdominal segments, which are, moreover, thickly covered with long hair. If, however, such an organ is present, it is decidedly extremely reduced. I have since been able to examine a male of the same species (*T. crinita* Dist.), thanks to the great kindness of Mr. F. Muir, and have found a very slight swelling on the ventro-lateral angle of the IInd tergite, but no external evidence that this is an audito capsule.

ε. *Other Sense-Organs.*

The antennæ bear a number of sense-organs or, rather, sensillæ, usually considered (Berlese, 1909) as olfactory, although I am not aware of any experimental evidence in support of this view. Hansen (1890) was the first to describe these. The second (and of course also the first) segment of the antennal peduncle lacks these organs entirely; but on the underside of the first and second segments of the flagellum there is a large number (text-fig. 69). Each is a pit with a blunt conical spike at the bottom. Hansen distinguished two different kinds—some fairly large, wide, and shallow, and others smaller and deep, the spikes hardly projecting from the orifice. A few of the smaller kind recur on the succeeding segments of the flagellum.

Text-figure 61.



Carineta formosa. Male: dorsal view of anterior portion of mesenteric sac and related parts.

mp., Malpighian tubules. (Other lettering as in text-fig. 60.)

Melampsalta sericea and *Magicicada septendecim* were examined by us. There the sensillæ are very numerous; all on the under surface, most on the first flagellar segment, but many also on the succeeding ones. Less difference between the two kinds than mentioned by Hansen was seen, and the type with projecting spike was found on other segments than the first, especially in *M. sericea*.

Berlese (1909) discusses and figures the antennal sensillæ in *Tibicen plebeia* (p. 620, fig. 745).

The tip of the rostrum in both nymphs and adults is furnished with numerous hairs which conceivably subserve a sensory function. At least such an hypothesis is more probable than the one held as recently as 1839 by Nathaniel Potter, who believed that moisture was absorbed through them or, rather, "exhalations of vegetable barks."

b. MUSCULAR SYSTEM.

A very detailed account of the musculature of *Tibicen plebeia* is given by Berlese (1909, Cap. 8, figs. 452, 464, 466, 481, 496–498) and compared with that of other types. The complexity of the trunk muscles in general is not dissimilar to that attained in Lepidoptera.

The muscles of the mouth-parts have been referred to in the account of these organs, as also those of the auditory and sound-producing apparatus in corresponding places.

For the general trunk muscles we refer to Berlese, as cited above.

The rectal sac is strongly muscular, expelling the waste liquid with considerable force as a thin jet.

The tymbal muscles form the largest and strongest pair of muscles in the cicada body.

c. RESPIRATORY SYSTEM.

α. Spiracles.

There has been much confusion concerning the number, position, and terminology of the spiracles, especially in Cicadidæ, but also in Hemiptera in general.

Dufour (1883, p. 258) recognized in *Cicada orni* six pairs situated ventrally at the internal side of a deep longitudinal fold. He described these "ostioles" as lacking peritremes and as placed on small, rounded, whitish, somewhat salient spots.

Packard* attributes to Hemiptera and Orthoptera two pairs of thoracic spiracles present on the two anterior segments. So far as we know, no one recently has suggested that the first spiracles belong to the prothorax.

Landois (1867, 1874) considered spiracle (3) to be a "Schrill-stigma," the efficient instrument in the song of the cicada The true sound-organs he considered functionless.

Schiödte, in 1870, indicated ten pairs of spiracles in all Hemiptera—three thoracic and seven abdominal, the former lying on the hinder edges of their corresponding segments.

Handlirsch, in 1899, from a study of the relative size of the spiracles and of the branching of the tracheæ decided that

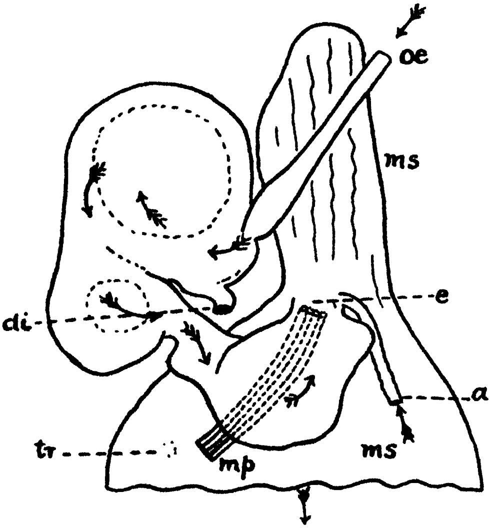
---

* "On the Distribution and Primitive Number of Spiracles in Insects," Amer. Nat. viii. pp. 531–534 (1874).

the third spiracle in Hemiptera was really the first abdominal. He found it in some cases on the hind border of the metathorax, in others on the intersegmental membrane, and in others on the first abdominal segment. The first abdominal segment he found was greatly reduced, and had been overlooked by taxonomists, who had practically universally called the second the first.

Heymons, in 1899, observed that in the nymphs of many species of Heteroptera the first spiracle is on the meso-, the second on the metathorax, and the third on the first abdominal segment, but in the course of development there is a movement forward, so that the first lies between the pro- and mesothorax, and the third on the metathorax. The first segment in the abdomen to show a stigma distinctly on its surface is the true second.

Text-figure 62.



Carineta formosa. Female: latero-dorsal view; the stomach slightly displaced. *e.*, entrance of Malpighian tubules into wall of stomach at junction with mesenteric sac; *tr.*, position of tracheal knot viewed from within. (Other lettering as in text-fig. 61.)

Hansen (1902, pp. 214–216, transl.) gave the first detailed description of cicada spiracles, though Handlirsch had studied the nymphal exuviæ of one form. Hansen's results may be summarized as follows:—

1. The first spiracle lies between pro- and mesothorax in the articular membrane. It is almost perpendicular.
2. Occupies a similar position between meso- and metathorax.

3. "The first pair of abdominal spiracles lies on the ventral side of the body close to the lateral margins in a depression at the base of the abdomen, surrounded by solid chitin (a part of the metasternum), which, particularly in the male, is very thick and of considerable breadth. They are transverse like the thoracic spiracles, but somewhat shorter than these. . ."

4. The second abdominal spiracle is on the underside of the body, facing forwards and towards the insect's middle plane.

5–10. "Each of the third to eighth abdominal spiracles lies in the sternite itself, a little behind its front margin. . ."

Spiracles 4–10 inclusive are considerably smaller than the others, and of different structure; they are entirely open, with an oval or almost circular orifice, the peritreme being a solid ring, which is also furnished with a great number of hairs directed towards the centre of the spiracle (Hansen, *l. c.* p. 216).

The condition in *Melampsalta muta* is as follows:—

We number the spiracles consecutively in one series, owing to the dispute as to whether number 3 is thoracic or abdominal.

1. As described by Hansen. The trunk entering from it is very large, but the spiracle itself difficult to see. It is very slit-like.

2. (Text-figs. 9, 22, *sp.* 2.) This is more rounded than (1) and lies in the intersegmental membrane between mesothorax and metathorax, just below base of tegmen.

3. (Text-figs. 16, *sp.* 3, 17, 18, 22.) This is just beneath outside angle of the operculum.

4. (Text-figs. 19, 20, 22, *sp.* 4.) This lies in close association with the auditory capsule, and is seen only in facial view in the untreated specimen. Hansen's description is good, except that the spiracle is really on segment I. (text-figs. 19–21; see later).

5–9. As described by Hansen. These are shown in text-fig. 11.

10. This is difficult to find. It lies in the intersegmental membrane in the angle between VIIIth tergite and VIIIth sternite (text-figs. 13, 35).

In *Thopha saccata* the 5th spiracles are covered with a white pruinose material, which, with their raised rims, renders them highly conspicuous.

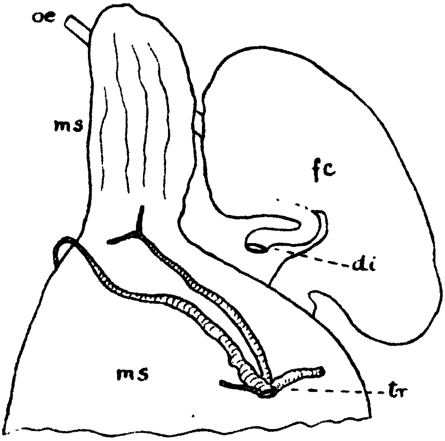
We are now concerned with the question as to whether the 3rd spiracle is thoracic or abdominal, as we have seen it has much more in common with the preceding (thoracic) ones than with the succeeding (abdominal).

Yet if we accept the evidence of Handlirsch and of Heymons, confirmed and accepted by Dogs in *Nepa* (1908), by Hagemann in *Corixa* (1910), by Hoppe in *Notonecta* (1911), and by Wefelscheid (1912) in *Plea*, it would appear that it is abdominal in origin. Moreover, the latter origin is almost a logical necessity unless we are prepared to admit a prothoracic spiracle. Hansen, who was the first to point out that spiracle 3 in Cicadidæ differed from the thoracic type, and who also expressly stated that it is surrounded by solid chitin of the metasternum, yet continued to call it *first abdominal*.

Crampton * subscribes to the theory of a forward migration of spiracles as described by Heymons. Snodgrass (1921, p. 403) refers to the spiracles lying just before the tymbals in a male cicada as those of the first abdominal segment. These are our sp. 3 (text-fig. 17). Kershaw and Muir (1922, pp. 202, 206) refer to the last spiracle as the eighth abdominal.

Vogel (1923) accepts Heymons's results and considers spiracle 3 as now definitely placed on the metathorax. He was the first to indicate that spiracle 4, in front of the auditory capsule, is topographically now attached to abdominal segment I., as shown in our text-figs. 19, 20, and 21, but by no means obvious unless a KOH preparation is made.

Text-figure 63.



Carineta formosa. Female: ventro-lateral view to show tracheal knot on surface of mesenteric sac. (Lettering as in text-figs. 61 and 62.)

Finally, Mammen (1912) agrees that spiracle 3 is to be considered first abdominal.

To avoid confusion it is best to number the spiracles consecutively in one series. Then and then only shall we know whether "metathoracic spiracle" is meant to imply 2 or 3.

The most detailed description of the spiracles themselves has been supplied by Mammen (1912). He studied the nymphal exuviæ of "*Cicada gigantea*" (= ? *Pomponia g.* Dist.) and the adult of a *Platypleura* sp. from Kiautschou (probably *P. kaempferi* (Fabr.)).

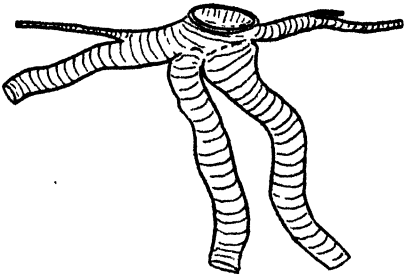
---

* Ann. Ent. Soc. Amer. xi. p. 356 (1918).

In the former he found the thoracic spiracles pleural, and the abdominal he considered to lie on the border of sternite and parasternite, in complicated folds. In essentials the closing apparatus is similar to that in adult *Platypleura.*

In the latter the first spiracle showed very interesting specializations. The mesothorax is anteriorly produced far forward into the prothorax, so that the projecting hind margin of the latter covers a more or less enclosed space (Luftraum) in which lies the spiracle in question. There is an intricate closing arrangement with a special muscle, and, in addition, a complicated system of hairs and bristles to prevent entrance of foreign bodies. This spiracle belongs to the type known as "Visierstigmen," *i. e.*, the spiracle has come to lie in an insinking of the intersegmental membrane, and this depression has taken up an oblique position so that the stigma does not lie directly beneath the opening of the pit.

Text-figure 64.



Carineta formosa. Tracheal knot of surface of mesenteric sac immediately beneath left third spiracle. External view.

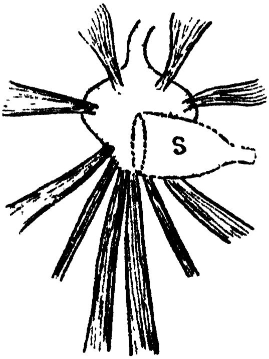
The second stigma lies between meso- and metathorax and belongs to Mammen's "Deckstigma" type, in which the fore-border of the spiracle forms a kind of lid which fits over the opening right to the hind edge, to which it may be tightly appressed by the contraction of a special closing muscle. Since this spiracle lies perpendicularly beneath the gap between two segments, the risk of entrance by foreign matter is great, but is obviated by the presence of numerous hairs and a chitinous plate which projects over the stigmatic opening from the fore edge of the metathorax.

The abdominal stigmata in this *Platypleura* lie laterally on the fore-border of each sternite, so that each is slightly overlaid by the posterior edge of the preceding segment. The first abdominal spiracle is situated under the hind edge of the metathorax in a complicated fold. In the abdominal segments, in general, the integument sinks in to form a hollow, at the bottom of which lies the stigmal opening. The hind wall of the hollow evaginates medially as a short, plump cone for the attachment of the closing muscles. Further details should be studied in Mammen's elaborate paper with the aid of his excellent figures.

β. *Tracheæ.*

The general tracheal system has received no comprehensive treatment since the work of Dufour (1833), who distinguished in *Cicada orni* two kinds of trachea—tubular and utricular. The first, he said, were distributed especially to the abdominal viscera and were very fine. Those ramifying among the digestive organs were enveloped in an adipose sheath; those in association with the genital system brilliant and shining. The thoracic cavity was said to have two moderately large trunks distributing branches as far as the salivary glands and the rest of the head.

Text-figure 65.



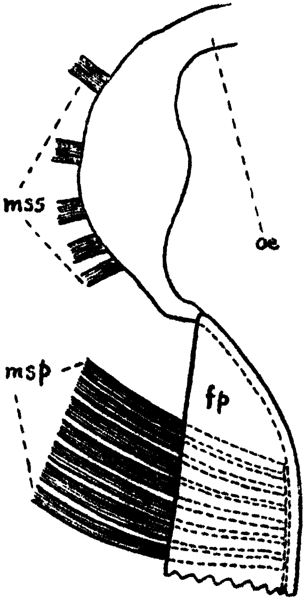
Carineta formosa. Male. dorsal view of enlargement of œsophagus, posterior to true sucking-pump, showing five pairs of dilator muscles and their position in relation to supra-œsophageal ganglion (*s.*).

Dufour describes the utricular tracheæ as, in general, small bullæ, some globular, others of diverse shapes, more or less grouped, especially on the lining membrane of the abdomen and on the surface of the thoracic muscle masses. Independent of these small bullæ there is a large conical utricle on each side of the mesothoracic cavity.

Dufour believed that, in general, very active insects show the greatest development of utricular tracheæ. He was therefore surprised to find so few in Cicadidæ, with their well-developed motor apparatus, but explains the deficiency by ascribing to these insects "des habitudes sédentaires."

A thoroughgoing study of the whole tracheal system is much needed, in view of the controversy as to whether the large abdominal sac is tracheal or mesenteric. We have referred to this before and shall not discuss it now, save to mention that we deal with it at length with the digestive system of which we think it a part, and to state that in the examples examined we were able to establish no other connection with the tracheal system than that afforded by a stout, short trachea from the third spiracle, running at once to the immediately adjacent surface of the sac and there, without penetrating, forming a tracheal knot (text-figs. 63, 64) which breaks up into several branches ramifying over the wall of the sac in question. This is the stigma, nevertheless, with which Snodgrass (1921 *b*) and Vogel (1923, p. 207) believe the sac to obtain its only communication with the outside.

Text-figure 66.



Carineta formosa. Entirely schematic longitudinal section of posterior part of pharynx and anterior portion of œsophagus.

mss., dilators of second swelling of food-canal; *msp.*, dilators of pharyngeal sucking-pump; *fp.*, frontal plate of tentorium; *œ.*, œsophagus.

Vogel (*l. c.*) claims that the usual communicating longitudinal and transverse tracheæ are absent in cicadas, at least in the third to eighth abdominal segments. Nevertheless, in *Fidicina* (text-fig. 26) we are able to find a wide transverse trunk running in the tergal arch between the fifth spiracles (third abdominal), and between the members of the same pair a finer ventral trachea.

From the immediately preceding spiracle a large trachea likewise arises, but branching soon, it fails to form a transverse trunk (text-figs. 25, 26).

The tracheæ of the seventh pair of abdominal spiracles are said to be devoted wholly to the service of the mycetomes, the elements of which are bound together into the semblance of an organ by their smaller branchlets.

That all the spiracles, apparently without exception, are, however, linked up by a longitudinal trunk on each side is obvious from an examination of the nymphal exuviæ. The connection between spiracles 1 and 2 is a particularly stout trachea.

To sum up, we know that there are transverse tracheæ between the spiracles of certain pairs, and longitudinal ones connecting the spiracles of each side. There is also a conical air-bladder on each side of the mesothoracic cavity. Further elucidation of the tracheal system must await the acquisition of fresh material for dissection.

d. ALIMENTARY SYSTEM.

a. Historical Review.

The widespread classical belief that cicadas lived only on dew was based probably on the absence of any striking signs of injury to the plants frequented by these insects, and partly no doubt on the lack of anything which the unskilled observer could recognize as an effective mouth.

The first name associated with an actual dissection of the cicada digestive system is one which "every schoolboy knows." Meckel, in 1808, gave a surprisingly detailed description and figure of conditions in *Tibicen plebeia.* He stated that the whole canal was at least ten times the length of the body. He distinguished œsophagus, stomach, "einen aus diesem entspringenden und in ihn zurückkehrenden langen Kanal," a long thin and a short thick intestine. The mesenteric sac is shown in its correct relationship, but the true intestine runs out of the œsophagus—probably he ruptured the thinner part of the stomach. The salivary glands were explained thus :—" Es sind offenbar Organe, die eine Feuchtigkeit absondern, welche der Cigale das Anbohren des Holzes erleichtert." (p. 3.)

The next worker was Ramdohr (1809, 1811), who largely followed Meckel so far as cicada anatomy was concerned, but appears to have discovered the suspensory "ligament" of the anterior projection of the mesenteric sac. This, however, seemed to him so anomalous that he regarded it "comme un tissu accidental et contre nature." (Dufour, 1825, p. 161.)

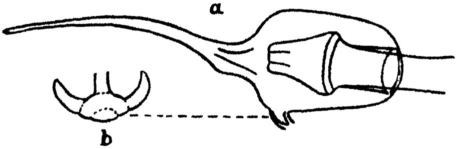
Marcel de Serres (1813) added little save the statement that the Malpighian tubules entered an enlarged part of the œsophagus.

With his great countryman Dufour, however, it was far otherwise. This observer laid the foundation for a knowledge of the internal anatomy not only in Hemiptera, but also in several other insect orders. In 1825 he described the main parts of the digestive system with great clarity, and claimed that "les Cicadaires sont jusqu'à ce jour les seuls insectes ou ce ligament suspenseur [of the mesenteric sac] existe." (p. 161.) He explained this latter as due largely to the habitual vertical position of these insects. In 1833 he published an amended account of the digestive system in *Cicada orni*. Perhaps the one point on which he was mistaken lay in supposing that the "intestiniform tube" in ascending opened into the cavity of the stomach rather than coursed merely in its walls.

The fact of the latter condition was established by Doyère in 1839 in a paper criticising Dufour's work and claiming, further, that the latter was incorrect in describing four Malpighian tubules since there were only two.

To this Dufour (1839) replied, accepting very gracefully the correction concerning the filter-chamber, but re-asserting his belief that there are four Malpighian tubules, in which of course he is abundantly confirmed.

Text-figure 67.



Melampsalta leptomera. Salivary pump.
a., lateral view of whole organ from left; *b.*, ventral view of entrance of salivary duct.

Lubbock (1859) described the "internal gland" of Coccids.

Later workers on cicadan splanchnology have been Schindler (1878), Nassonow (1899), Quaintance (1902), Gadd (1902, 1910), Hargitt (1903, 1923), Licent (1911 *a*, 1911 *b*, 1912), Berlese (1909), Kershaw (1913, 1914), Hickernell (1920, 1923), Snodgrass (1921 *b*). Gadd's paper (1910) is of great value in that it gives comparative data on eight species in the genera *Tibicen*, *Cicada*, *Cicadatra*, and *Melampsalta*.

Burnett (1851) claimed that in *Magicicada septendecim* there was no trace of the digestive system in the male. Later American entomologists, even as recent as J. B. Smith, believed that the gut was more or less atrophied in this species.

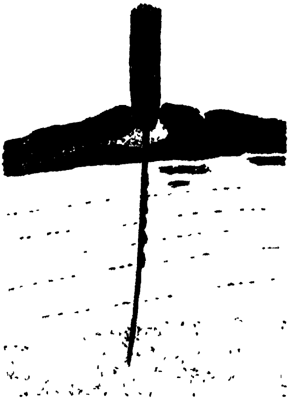
Finally, there are those who, like Carus and Graber, interested primarily in the sound-producing apparatus, took the mesenteric sac for an air-bladder of the tracheal system. Apparently the only one who has held to this belief after dissecting the alimentary tract is Snodgrass (1921 *b*). All the other workers cited above have given an interpretation, with which, in essentials, the account set out in the following pages will be found to agree.

β. General View.

It will conduce to the clarity of the succeeding account if we prefix it with a sketch of the salient points of the whole digestive tract (text-fig. 60).

Functionally the first part of the alimentary canal consists in cicadas, as in all other Hemiptera, of an extremely fine passage between the closely-apposed mouth-setæ, which are themselves enclosed in the trough-like rostrum. Soon after entering the head the food passage widens into a capacious and powerful sucking-pump, a dilated portion of the pharynx, which is succeeded by a smaller but muscular swelling just below the entrance to the thorax. At the posterior extremity of the thorax the œsophagus enters the peculiar complex known first by Lubbock as the internal gland (in Coccids), but now more generally termed the filter-chamber. The essence of this arrangement consists in the zig-zagging of the ascending part of the mid-intestine in close association with the attached portions of the Malpighian tubules in the actual walls of the anterior part of the stomach. By this construction it is believed that the watery constituents of the plant sap (Licent), or these and the surplus sugars (Berlese), pass directly by dialysis through the lining of the stomach and the walls of the intestine, and thus are carried direct by the rectum to the exterior; while the more nutritious elements are selected to pass by the more circuitous digestive route. The forepart of the intestine thus forms a long and very intricately coiled loop which appears finally to end in the stomach, as indeed Dufour originally believed it to do. The position, already complicated by the serpentine twistings of the intestines and

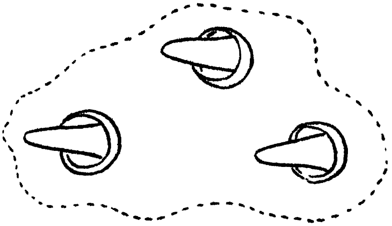
Text-figure 68.



Magicicada septendecim. Stylets inserted in branch (from Quaintance, 1902).

Malpighian tubules, is further obscured in cicada by the extraordinary development of a huge, thin-walled, mesenteric sac, occupying most of the abdominal cavity in the male and considered by Graber, Snodgrass, and many others as an air-sac of the tracheal system. It is, however, a part of the stomach in direct communication with the cavity of the interior part of the latter (not merely of the filter-chamber), and gives rise at its own posterior extremity to the ascending mid-intestine, which, after many convolutions, enters the main stomach-wall near the junction of this main stomach with the mesenteric sac. After a tortuous course within the walls this tube receives the Malpighian tubules which have accompanied it within the investment of the stomach, then joins the posterior intestine at the anterior end of the stomach, which it leaves near the entrance of the œsophagus, and proceeds after much winding to the muscular rectal sac which opens to the exterior on segment X.

Text-figure 69.



Magicicada septendecim. Sensillæ of first antennal flagellar segment.

The salivary glands appear as bunches of lobules filling the greater part of the head-cavity. Their deferent canals unite to form a single duct carrying the salivary secretion to the salivary pump or syringe, which forces it down the smaller of the two maxillary channels into the pierced plant-tissue. The juice from the latter is sucked up the larger or food-canal formed by the close apposition of the maxillary setæ.

γ. *Morphology.*

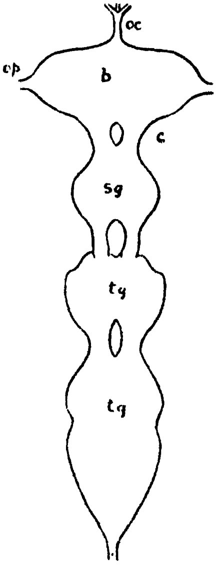
i. *Mouth and its Appendages.*

The food-passage begins with the mouth, but it is largely an academic question where the mouth lies. Bugnion and Popoff (1911) consider it to be at the tip of the rostrum: and functionally the entrance of the tube between the apposed maxillary setæ must be the mouth, even when the stylets are sunk in tissue far beyond the tip of the labium (text-fig. 68). Embryologically the opening of the stomodæum corresponds, however, to the egress pore of the stylets from the head-capsule before they enter the [illegible] As shown by Snodgrass, this is the functional relic of a very wide orifice which extends between the apposed edges of the epipharynx and hypopharynx. Into this mouth-pore opens a short, narrow tube, found by Meek to be strongly chitinized, which is the beginning of the pharynx; and to this same spot the efferent duct of the salivary pump, opening actually at the tip of the hypopharynx, delivers the salivary juices.

ii. *Pharynx.*

Following the narrow, chitinized tube is an extremely wide chamber lying in the boat-shaped chitinous trough formed largely by the frontal plate of the tentorium. This is the sucking-pump. At rest the dorsal wall, which is strongly invaginated, touches the floor, which is fused both in old nymphs and in adults to the chitinous substance of the frontal plate, though Muir says it may be separated in a nymph just after ecdysis, before the chitin has hardened. Thus the whole of this pharyngeal chamber, despite the commonly-accepted opinion, is membranous except for a

Text-figure 70.

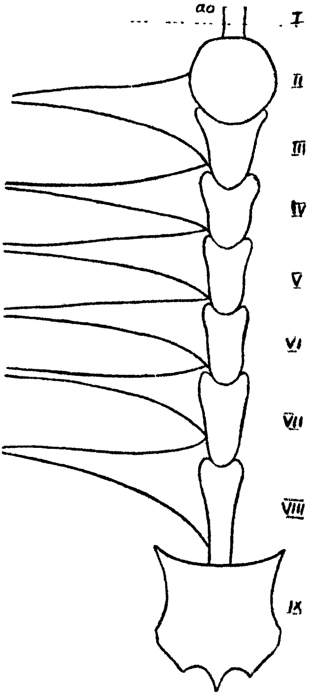


Melampsalta sericea. Male: dorsal view of chief ganglia of central nervous system; drawn in one plane.

oc., common stem of ocellar nerves; *op.*, optic nerve; *b.*, supra-œsophageal ganglion; *c.*, œsophageal connective; *sg.*, sub-œsophageal ganglion; *tg.*, ganglionic masses of thorax.

chitinous median longitudinal portion of the deeply invaginated dorsal wall. Here are inserted the very numerous and feathery muscles which are attached to the inner surface of the swollen frons, whose striations correspond with the attachments of these muscles (text-fig. 66). In the nymph of *Melampsalta cingulata*, and probably in others, the front is much more swollen and smoother than in the adult, but the striations are marked with lines of bristles which are used as a cleaning apparatus for the fossorial fore-limbs. Snodgrass considers this sucking-pump a part of the mouth-cavity and not of the true pharynx (1927). He is led to this view chiefly by his belief that a true pharynx is always a muscle-covered organ, whereas the dilation under discussion is membranous and chitinous, its only muscles being the dilators of the roof. He finds that the dilators of the mouth-cavity are mostly attached to the clypeus in other insects. This would make the striated facial place, called by us the frons, really

Text-figure 71.



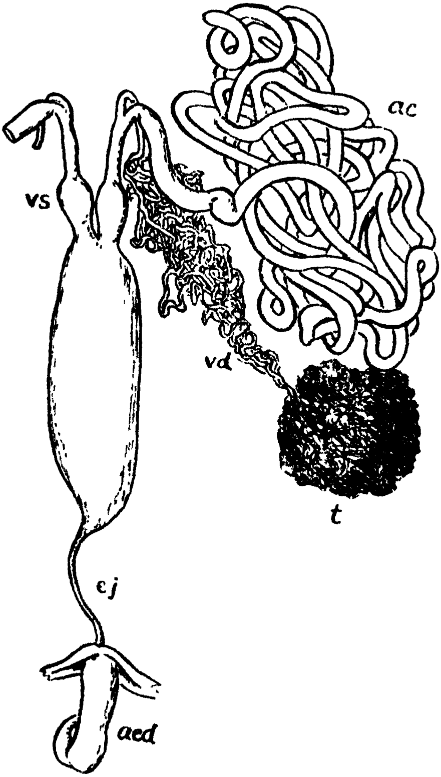
Carineta formosa. **Male: dorsal view of dorsal vessel.**

I.–IX., abdominal segments; *ao.*, aorta.

the clypeus. Meek describes the pharynx or sucking-pump as formed by two troughs, one lying within the other—a very apt illustration.

The sucking-pump leads backward into a narrow tube, which, just above the tentorium, dilates once more to form a strongly muscular sac, shown by Snodgrass (1921 *b*, fig. 6), but apparently missed by Meek. It was then considered by Snodgrass as a second bulb, but he now (1927) believes it to be the true pharynx. It is provided with numerous dilators of which the distribution is somewhat obscure (text-figs. 65, 66). Thus Snodgrass in *Magicicada septendecim* found the first dorsal dilator muscle to go to the neighbourhood of the median ocellus, the second to the dorsal arms of the tentorium, the third to the lateral parts of the

Text-figure 72.

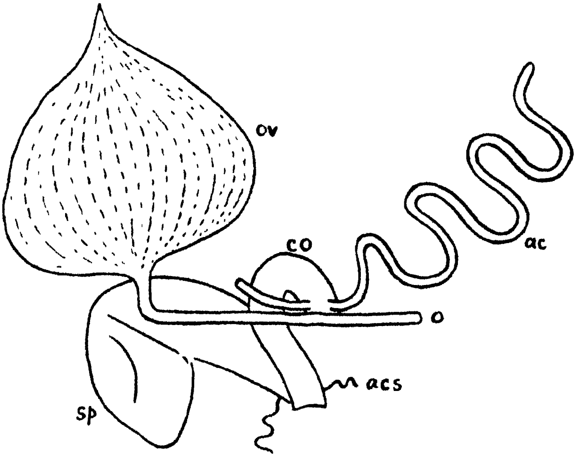


Carineta formosa. Male reproductive organs, semi-dorsal view.

t., right testis; *vd.*, right vas deferens; *vs.*, left vesicula seminalis; *ej.*, ejaculatory duct; *æd.*, ædeagus; *ac.*, right accessory gland.

vertex, and the fourth to the occipital margin. In addition he saw two pairs of lateral muscles proceeding to the posterior arm of the tentorium. The brain was found to lie on the surface of the organ *before* the first dilators. This was taken as evidence that several anterior dilator muscles of biting-insects are here suppressed, since these ordinarily arise from between the bands of circular muscles, the absence of which in the sucking-pump makes Snodgrass deny its identity with the pharynx, extending some distance in front of the ganglion. But in the Paraguayan *Carineta formosa* (text-fig. 65) studied by us, while the distribution of the dilator muscles on this second enlargement agreed in the main with Snodgrass's notes on *septendecim*, yet the brain was ensconced on the surface of the swelling distinctly behind the roots of a group of at least two pairs of dorsal dilators. The posterior dorsal dilator muscles are in close relation with the anterior extremity of the aorta.

Text-figure 73.



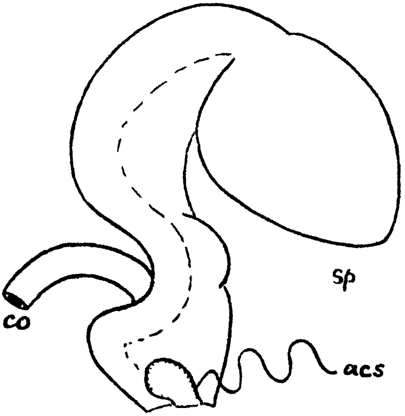
Carineta formosa. Female reproductive organs, ventral view.
ov., right ovary; *o.*, left oviduct; *ac.*, left accessory gland; *co.*, common oviduct; *sp.*, spermatheca; *acs.*, basal portion of left spermathecal gland.

iii. *Œsophagus.*

Behind the second enlargement, and just before entering the thorax, the food-canal, now the œsophagus, makes a sudden downward bend so that the subœsophageal ganglion is directly anterior to it. Through the thorax the œsophagus, tightly enclosed between the great lateral muscle masses, shows little differentiation, although Snodgrass (1921 *b*) describes and figures in *Magicicada septendecim* a transversely-corrugated distensible crop or proventriculus. Such a structure, if present at all, is very much less developed in *Carineta formosa.*

At the entrance into the stomach is the very effective œsophageal valve. Following Licent (1912) and Kershaw, we regard the remainder of the alimentary tract to the pyloric valve as mesenteric in origin. Hickernell apparently does not accept these as landmarks, since (1920, p. 226) he states that in cicadas "it is difficult to recognize the boundaries of the fore, mid, and hind guts." In stating that the whole of the canal between the œsophageal valves and the pyloric valves is mesenteric in origin, I do not wish to claim that this portion is derived entirely from endoderm, but rather that it does not form part of the embryonic invaginations, stomodæal and proctodæal. Kershaw (1913, p. 176) considers that in *Siphanta acuta* at least a part of this tract may be ectodermal in origin. The whole of the region thus delimited is lined with bare epithelium rather than with chitin.

Text-figure 74.



Carineta formosa. Female: part of reproductive system, ventral view. (Lettering as in text-fig. 73.)

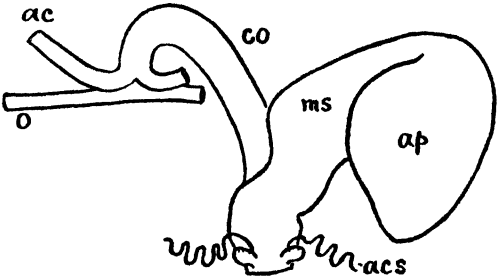
iv. *Stomach and Filter-chamber.*

At the junction of thorax and abdomen, or a little before, the œsophagus enters the stomach, the entrance being guarded by a valve. In *Carineta* part of the stomach may lie even in the thoracic cavity before the mesophragma.

The stomach (text-figs. 60–63) appears as a bilobed sac, called by Hickernell the anterior crop and by Kershaw the pouch or filter-chamber. The œsophagus enters the anterior lobe slightly beneath and behind its anterior end (text-fig. 62). The first lobe is opaque, apparently muscular, and with an irregular surface, while the second is rather thin-walled and spherical. By the position of the œsophageal valves this stomach must be considered part of the mesenteron, as Licent, Kershaw, and Snodgrass seem to agree. In some of the other Auchenorrhyncha, and especially the Cicadellidæ (Jassoidea), the anterior chamber forms a much more distinct diverticulum of the stomach, and is there called by Licent the *poche*. It would seem to be homologous with the huge anterior diverticulum which Kershaw found to extend into the cephalic horn of lantern-flies and other Fulgoroids, but these insects differ from most of the other families of the Auchenorrhyncha in lacking a filter-chamber altogether.

The condition of the stomach in the Paraguayan *Carineta formosa* is not quite like that of any hitherto described species, but resembles nearest the figure (pl. 4. fig. 5) given by Kershaw (1914) of an undetermined Trinidad form. It may be best comprehended by reference to text-figs. 60–63. Although it curves collar-like in a very intimate manner partially around the anterior portion of the mesenteric sac, it does not communicate with the cavity of the latter until near its own extremity closely adjacent to the spot where it receives the mid-intestine on its way from the posterior end of the mesenteric sac. The course of the mid- or ascending intestine in the thin wall of the second lobe of the stomach is relatively simple, and may be followed with ease from the outside ventral aspect. The four Malpighian tubes enter near the same spot, on the wall of the passage between the stomach and the mesenteric sac, but they are dorsal in position and run almost directly into the thick wall of the first part of the stomach, where they are immediately lost to sight. The course of the intestine and Malpighian tubules within the wall of the filter-chamber or first stomach-lobe is difficult to follow. Their coils are extremely thin-walled. Here it is that the chief arrangements of the filter-chamber function. The loops and zigzags of the intestine within the chamber are,

Text-figure 75.



Carineta formosa. As text-fig. 74, but dorsal view.
ap., apical pouch of spermatheca ; *ms.*, muscular proximal part of spermatheca.

however, much less complicated and numerous in Cicadidæ than in Cercopidæ, where the peak of evolution in this matter is reached. Both Licent and Kershaw confirm this independently. In *Carineta formosa* the intestine keeps rather closely to the anterior and ventral wall of the stomach, passing, however, dorsad of, and anterior to, the entrance of the œsophagus, and then curving round, receiving the Malpighian tubules and passing out of the stomach-wall as the hind or descending intestine. The Malpighian tubules follow a more dorsal course.

The condition in Cicadidæ is somewhat peculiar. They

> "montrent une structure de l'épithélium des lacets intestinaux toute differente à la fois de celle des Cercopidæ et de celle des autres insectes du groupe. . . . Les lacets [folds of the mid-intestine within the filter-chamber] à cause de leur développement, peuvent bien filter l'eau, mais leur épithélium a l'air beaucoup moins specialisé dans cette fonction que celui de toutes les autres cicadines à poche." (Licent, 1912, p. 88.)

We have considered throughout, as dissection seems to show and as Licent asserts, that the intestine and the Malpighian tubules in the filter-chamber are actually in the wall of the stomach between the epithelium of its lumen and the external muscular investment. But Kershaw (1914, p. 66) explains the condition differently, as follows:—

> "The zigzags of the various parts of the gut do not pierce the walls of the pouch in order to enter or leave it, but are merely enclosed between its exterior wall, the peritoneal membrane, muscular and connective tissues sealing up their entrances and exits and the narrow gap or slit-like opening between the exterior walls of the pouch."

Hickernell (1920) expressed somewhat the same view, but the distinction is largely a merely verbal one, since the peritoneal membrane of the stomach (pouch) is, after all, a part of its investment. The striking feature anatomically is that the membrane separating the very thin-walled intestinal and Malpighian filter coils from the lumen of the stomach is extremely thin.

Muir (1923, p. 213) credits all the Auchenorrhyncha except the Cicadellidæ and the Fulgoroidea, and all the Sternorrhyncha without exception, with a filter-chamber, and draws phylogenetic conclusions therefrom, on the assumption that such a structure probably did not arise more than once. But Licent has shown that, though the filter-chamber may be physiologically similar throughout these groups, it differs greatly morphologically. The divergence between Auchenorrhynchous and Sternorrhynchous conditions is especially great, as Licent remarks (1912, p. 29):—

> "Il est absolument impossible, au point de vue anatomique d'assimiler à aucun degré, à ces formations des Coccidæ, la poche des homoptères supérieurs dans laquelle l'œsophage ni le rectum ne sont absolument pas engagés."

Similarly, Hickernell (1923, p. 214) says:—

> "Berlese (1909) describes the digestive organs of certain scale insects. In these insects the rectum is large and extends anteriorly as far as the œsophagus. This results in a knitting together of rectum and œsophagus, and also causes the intestine to describe a complete circuit of the abdominal cavity before it finally joins the rectum. This condition, while resembling it superficially, is entirely different from the arrangement found in the adult cicada, since in the latter the relatively enormous enlargement affects the midgut, while the rectum is small."

Hickernell (1923) found that the filter-chamber is typically developed, even in the newly-hatched nymphs, a result to be expected from the similarity in feeding-habits throughout the life-history; so this condition evidently arises in the embryo.

v. *The Mesenteric Sac.*

This is one of the most disputed organs of cicadan anatomy. By far the greater part of the abdominal cavity, often in both sexes, but especially in the male, is taken up by a huge thin-walled sac (text-fig. 60, *ms.*) of which the greatly wrinkled anterior portion is wedged in the V between the two large tymbal muscles, and is produced into a horn extending into the thorax and suspended from the œsophagus by a tendinous band. This is the sac which Graber (1876, pl. i. fig. 5, *Be.*) and Snodgrass (1921) claim as part of the tracheal system, while Vogel (1923) believes it accessory to the auditory organ; but in the South American *Carineta formosa* I find that not only has it no connection with the tracheal system, but that it also opens widely and definitely into the anterior part of the posterior portion of the stomach, thus confirming the views of Dufour, Doyère, Nassonow, Gadd, Licent, Kershaw, Hargitt, and Hickernell. Licent calls it *le segment conique* of the *dilation ventriculaire*; Kershaw refers to it as a sac of the midgut; while Hickernell names it *posterior crop*. Snodgrass (1921, p. 403) considered that this sac, as a part of the tracheal system, received its air-supply directly through the first abdominal spiracles (sp. 3), which lie just before the tympana, but Hickernell (1923, p. 220) writes:—

> "It is easy to be deceived as to the continuity of the lumen of the posterior crop with the exterior through these first abdominal spiracles. In gross dissections there is only the most delicate epithelial membrane limiting this abdominal sac in the region of these spiracles. . . . If a specimen is allowed to become dry, the portion of the wall which is in front of the spiracular opening may easily rupture, and then there is an external opening in fact. Sections show that the spiracle opens into a very small chamber the walls of which break up almost immediately into a number of tracheal tubes [text-figs. 67, 68] which distribute themselves over the external surface of the posterior crop. I am therefore still inclined to

> question any interpretation which gives this organ a respiratory function. It certainly becomes modified in later life, but it is at all times a part of the digestive system. This condition, which is easily observed in sections, makes unnecessary the postulation of any secondarily derived function on the part of this organ. The method of gross dissection, then, is inadequate to explain the conditions found."

Hickernell further notes that the interior of a tracheal sac should have a chitinous lining, while sections demonstrate conclusively that the present organ is lined with epithelium, although in the middle portion the walls become so extremely thin that the cells may be cuboid or even squamous instead of columnar.

Our gross dissections (text-figs. 63, 64) and those of Lucas (1887) confirm Hickernell's results concerning the relation between the third spiracle and the adjacent wall of the mesenteric sac. These relations are so close that we suppose it within the bounds of possibility for the sac thus to gain an opening with the exterior similar to that described by Snodgrass. But the fact would nevertheless remain that the connections with the rest of the digestive system are primary and fundamental, and the communication of the mesenteron with the exterior through the body-wall direct would constitute a condition so anomalous that the proof required to establish it would be almost as rigorous as that demanded by Huxley for the presence of a unicorn trotting down the Strand.

With regard to the extent of the sac, Hickernell found in extreme cases that it went back as far as the VIth segment. In *Carineta*, in the male at least, its development is greater still. Hickernell ascertained that the size of the sac increases not only with the life of the adult insect, especially with decrease in size of the fat-body, but also throughout ontogeny. In the nymph (1923) it is much smaller and considerably folded, with a tortuous lumen. In the adult male, as noted first by Hickernell, its walls may closely approach the actual integument on all sides, leaving extremely little space in the main part of the abdomen for the organs of circulation and reproduction, and for the profuse coils of the intestines and Malpighian tubules, all of which, as Snodgrass puts it, are in places jammed in a space no thicker than a piece of paper. Hickernell is inclined to homologise this great saccular diverticulum with the prolongation described by Kershaw in Fulgoroids and stated in his earlier work to arise from the œsophagus. But although this latter has also been shown now to be of mesenteric origin, yet both Kershaw (1914) and Licent (1912) agree in homologising it with the *poche* or filter-chamber of the columate Auchenorrhyncha. There is certainly no doubt that the two organs are morphologically dissimilar in origin, though both mesenteric, but whether they may not serve the same function is another question. Licent shows in a very instructive manner that throughout the

Auchenorrhyncha* the mesenteric sac (*Segment conique*) increases in size with reduction of the filter-chamber. Thus the former is large in Cicadidæ, where the filter-chamber is somewhat reduced, while in Typhlocybids, where the latter is altogether absent, the sac becomes simply enormous.

vi. *The Mid-intestine.*

The part of the alimentary tract now to be considered is called by Licent the *mediintestin*, of which the free portion forms the *boucle mediintestinale* or the *anse mediintestinale*. Snodgrass names it "the tubular continuation of the stomach," Kershaw simply "midgut," and Hickernell "ascending intestine." Among the coils of intestines and Malpighian tubules coating the exterior of the mesenteric sac the portions pertaining to the mid-intestine may be distinguished macroscopically from those of the Malpighian vessels by their larger calibre and smoother surface, and from those of the hind-intestine by their colour, as remarked by Dufour in 1833. Similarly, Nassonow found it crammed with yellowish granules. At the posterior extremity of the mesenteric sac is a knot of yellow tubes consisting of the first portions of the mid-intestine. This may be unravelled and the continuity of the mesenteric sac and the mid-intestine may be demonstrated, but the lumen of the latter is so minute that the actual communication can be confirmed only by sectioning, as has been done by Hickernell, Licent, and Gadd, while Kershaw shows the same passage in his figures (1914, pl. 4. fig. 5). The numerous and complicated yellow folds of the mid-intestine disentangle themselves eventually from the intermingled fat and Malpighian tubes, and the distal portion enters the filter-chamber, as described in the account of that organ.

Licent found that the mid-intestinal loop in the Cercopidæ showed a constriction near the end of its proximal third. Gadd (1902) believed that this constituted an actual stoppage, and regarded, therefore, the whole loop as two cæca joined at their distal extremities. But Licent demonstrated histologically that while the two portions were different in structure and apparently also in function, yet the lumen was never entirely blocked at the constriction as stated to be the case by Gadd. Nassonow had earlier found the lumen continuous in the Cicadidæ, and Licent discovered far less histological differentation between the two parts in this family. Such may be regarded as a more primitive condition than that prevailing in the Cercopidæ and most other columate Auchenorrhyncha.

The mid-intestine is joined by the Malpighian tubules just before the pyloric valve, which in most of the Auchenorrhyncha is marked by an externally visible swelling, but which in Cicadidæ seems not to have been noticed.

---

* Licent persists in calling the Auchenorrhyncha "*Homoptères supérieurs.*" If "height" means anything at all phylogenetically it connotes specialization, and the Sternorrhyncha are very much the most highly specialized of all Homoptera, albeit it is in many respects a specialization by reduction.

vii. *Hind-intestine and Rectum.*

The hind-intestine as it issues from the filter-chamber is grey, and easily distinguishable, even in its most complicated coils, from the bright yellow mid-intestine. In *Carineta formosa* its distal extremity enters the strongly muscular, pear-shaped, rectal sac nearer the "stalk" of the latter than in *Magicicada septendecim*, as figured by Snodgrass and by Hickernell (see our text-fig. 60). The rectum is confined to segments VIII. to X. (or XI.), and lies very close to the dorsal integument. As Licent remarks:—

> "La forte musculature de cette poche explique surabondamment l'énergie avec laquelle les homoptères étudiés en ces pages projettent les goutelettes pleines qu'ils évacuent par l'anus en si grand abondance."

Nassonow describes the little twist made by the hind-intestine as it enters the rectal pouch. In this twist are incorporated the distal extremities of the Malpighian tubules.

viii. *Salivary Glands and Pump.*

The first detailed description of the salivary glands in Cicadidæ is apparently that of Dufour (1825), amended in 1833. His account is remarkably accurate.

Many writers have been fascinated by the salivary pump of Hemiptera, and since this organ shows little variation in essentials, their descriptions are largely applicable to Cicadidæ.

In 1910 Bugnion and Popoff studied in detail the salivary glands of numerous representatives of the order, and concluded with a description of conditions in *Cicada orni*. This has been in part confirmed by Snodgrass (1921) in *Magicicada septendecim*, and by me in *Carineta formosa* and in several New Zealand species of *Melampsalta*.

The glands form whitish digitiform lobules clustered in bunches and filling most of the head-cavity between the muscles, and extend also into the prothorax. There is an anterior pair forming the chief gland which supplies the principal canal, and a posterior pair—the accessory or aberrant gland—joined to the first by a short thick cord on each side. A third gland pair, consisting of a long filiform organ on each side with a small spheroid body in its course, joins the principal canal near its origin. There are thus, on each side, three canals meeting at the same place on the deep face of each principal gland.

The principal gland exhibits two kinds of digitations—larger ones to the number of sixteen or twenty and white in colour, and smaller ones more or less transparent. Among the former, in *Carineta* we found several lobules (*acini*) similar in structure to the white ones, but deep black in colour. These were irregularly distributed among the others.

The principal canal unites, after a very short course, with that of the opposite side, and the common trunk runs to the salivary pump. In *Melampsalta leptomera* (text-fig. 67) its entrance into the antero-ventral wall of the pump-chamber is flanked by two short, stout, curved transparent horns. In *Cicada orni* the debouchure is similar in position and marked by a rounded swelling. In *Magicicada*, while Meek shows it similar here also, Snodgrass (1921 *a*, p. 6) states that the "common duct appears to open at the very tip of the terminal point of the hypopharynx." This is surely an error. Gadd (1909, fig. 2) shows in *Cicadatra atra* a condition identical with that in *Melampsalta leptomera*.

The aberrant gland contains a score of lobules similar to those of the principal gland, but a little larger, more transparent, and easier to isolate. The cord joining it to the principal gland has an opaque covering, formed largely of tracheæ (Bugnion & Popoff).

The filiform organ is a very fine and delicate tube, in *orni* about 20 mm. long. Beginning with a free, rounded, blind extremity it makes many turnings behind the head and then joins the principal gland at its origin. Composed of the two distinct segments, it shows in its distal part a relatively wide tube with thick walls, furnished internally with cells badly delimited and difficult to distinguish (B. & P.). The proximal segment, much shorter, has a chitinous canal surrounded by a thin investment like that of the collecting canals in general. At the junction of the two segments is a small rosette containing some atrophied glandular lobules. Bugnion and Popoff consider that this peculiar *aberrant gland*, discovered by Dufour in 1825, takes the place of the great abdominal salivary gland of "Fulgora."

The salivary pump is a tiny but tough chitinous cylinder or elongate bell of transparent material lying beneath the trough-like frontal plate. The piston or plunger (text-fig. 67), striated deeply but sparingly in both *Melampsalta leptomera* and *Cicada orni* (B. & P.), is darker in colour. The pump anteriorly * continues into a narrow heavily-chitinized tube opening near the mouth-pore. Posteriorly the shaft of the plunger expands into two branches, each serving for the insertion of a wide and powerful protractor muscle.

Muir and Kershaw (1911, p. 79) have shown that the salivary pump is a differentiated part of the common salivary duct, from which it arises in the embryo.

As regards the histological structure, Bugnion and Popoff found that the glandular digitations show an external cuticle supporting tracheæ, and in the interior a greyish cytoplasm without distinct cell-limits, and a branched nucleus. There is, to all appearances, a single nucleus or acinus in spite of its relatively large dimensions. The presence of these ramified nuclei gives to fresh pieces in saline a peculiar aspect; the terminal nuclear branches being a little dilated, one sees in each lobule a great number of small swellings joined to one another by straight bridges. Finally, above the great ramified nucleus there are small multiple nuclei situated at the surface of the acinus and pertaining to the small flat cells just beneath the cuticle and concerned in its production.

---

* In the hypothetical position, with the head of the insect porrect. Perhaps "cephalad" would be a clearer term.

Although ramified nuclei of the kind described in Cicada are characteristic of insect salivary glands in general, yet the Gymnocerate Heteroptera, studied by Bugnion and Popoff, show only simple oval or rounded nuclei in the salivary acini. This is a great divergence within the same order, and one would be interested to see how widely it extends.

Bugnion and Popoff's remarks on the phylogenetic development of the Hemipterous salivary glands are to be largely discounted by the fact that they regard the highly-specialized Aphididæ as lower forms, and seek to derive the condition in *Cicada*, *Fulgora*, and the Heteroptera from that in Aphides. The latter may have retained a primitive condition in this respect, but there must be no *a priori* assumption that such is the case.

Gadd's work on *Tibicen plebeia*, *Cicada orni*, *Cicadatra atra*, *C. hyalina*, and *Melampsalta montana* seems to agree largely with that of Bugnion and Popoff.

ix. *Malpighian Tubules.*

In the Cicadidæ the relationships and even the number of the Malpighian tubules are more obscured, firstly by their extreme length, secondly by their participation in the mesenteric complex known as the filter-chamber, and thirdly by the inextricable mingling of their distal extremities in the final knot of the hind-intestine just as it enters the rectum. From this point the tubules zigzag over the surface of the mesenteric sac until they enter the wall of the stomach near the entrance of the mid-intestine. The distal portion of the tubules is much thinner than the proximal, as shown by Licent in *Cicada orni* (1912, fig. 28). In the proximal portion, just after emergence from the filter-chamber, the narrow first part is succeeded by a very short, smooth, rather swollen section, apparently homologous with a more noticeable swelling, greatly developed in Cercopidæ and responsible for the secretion of the viscid material, which gives tenacity to their foam or "cuckoo-spit." The remainder of the tubule is varicose.

The Malpighian tubules are four in number, but after serpentining in the filter-chamber, and just before joining the mid-intestine near its junction with the hind-intestine, two, according to Licent and to Nassonow, remain free, while the other two fuse into a ureter—a very unusual condition found by Gadd and by Licent to occur also in the Cercopidæ. But in *Septendecim*, Snodgrass (1921 *b*) found that both pairs fuse, so that only two ureters join the intestine instead of one ureter and two tubules; while Kershaw (1914, pl. 4. fig. 5) shows the same condition very clearly in an undetermined Trinidad cicada.

The histology of the Malpighian tubules is considered at great length by Licent (1912). His masterly work should be consulted by all interested in the digestive system of Homoptera. An interesting feature is mentioned by Hickernell (1920, p. 236):—

> "At the point where the tubules enter the 'internal gland' there is an abrupt change in the character of their walls. They become thin, the nuclei decrease in size and are less chromatic. They retain their membranous character until they finally empty into the intestine near the anterior margin of the 'internal gland,' at the junction of the ascending and descending intestine."

At the same time their lumen increases greatly in size—all of which is highly significant, in view of the supposed function of the filter-chamber.

x. *Other Annexed Glands.*

The "excrementitious glands" of Dufour (1833, footnote, p. 225) are almost certainly the mycetomes, which house supposedly symbiotic fungi. The liquid squirted from the anus, and derived by Dufour from these glands, is obviously ordinary digestive waste, expelled by the contraction of the muscular rectal pouch.

δ. *Physiology.*

One still frequently sees it stated in entomological works that the rostrum is inserted into the tissues of prey, or food-plant, as the case may be. This is an entirely false assumption (see Myers, 1921 *c*). The rostrum or labium serves solely as a sheath, or in some cases (Psyllids) as a manipulator, of the setæ. When the latter are deeply inserted, the labium must be shortened or else bent back at one or more of the articulations. The former method occurs in cicada, where the setæ are not so excessively longer than the rostrum. The mandibular setæ apparently retain the whole setal organ in position in the tissues, while the maxillary setæ form the connecting channel. In the salivary pump the retractor muscles of the piston draw back the organ, causing saliva to enter the pump-cylinder from the duct-opening in the ventral wall. Thereupon the muscles relax, and the piston tends to return to its former position by virtue of the elasticity of the strongly chitinous wall. This forces the saliva down the smaller of the two maxillary channels, and thus into the food-tissue. Snodgrass (1921 *a*, p. 6) apparently missed this smaller passage, and was thus at a loss to understand that further pumping did not counteract the upward flow of the food-liquid. The function of the saliva remains still problematical; it may be solvent or digestive, or both. Meek (1903), following Plateau, considers the second function predominant. Bugnion and Popoff (1908) consider that a diastase is present which dissolves cellulose cell-walls and begins the digestion of starch grains. The combined effect, by whatever method, is doubtless a readier flow of sap. The reaction of the salivary secretion, according to Plateau, Bugnion and Popoff, and Kershaw (Cercopidæ), is alkaline.

The sap ascends the larger of the two maxillary canals, under suction by the great pharyngeal pump, exercised by the action of its dorsal dilator muscles. Snodgrass finds that on relaxation of these muscles the anterior end of the pump closes first, thus ensuring the retention of the liquid; and doubtless the second pharyngeal swelling, with its powerful dilators, acts in conjunction. The return of the dorsal wall of the pump would seem to take place by the elasticity of the chitinous supports and possibly by the chitinous dorsal rod, and not, as Muir (1926) suggests, by the reverse action of the dilator muscles, which would be hardly possible.

So much is fairly clear. We have the sap, more or less altered, in the œsophagus. It enters the filter-chamber through the œsophageal valve, and the problematical begins. Berlese has suggested for the Coccid filter-chamber—the internal gland of Lubbock—that by its means the water and the excess of sugars in the sap may soak through the *walls* of the coil into the rectum and thus take a short cut to the anus, while the more nutritious matters follow, as usual, the whole course of the alimentary canal. Kershaw (1913, p. 177) notes that feeding the insects (in this case the Flatid, *Siphanta*) on coloured liquids "tends to confirm this theory, since the contents of the long loop of the midgut are very faintly, if at all, tinted, whilst the rectum is heavily coloured." But neither of these examples deals with the true filter-chamber of the Auchenorrhyncha, as exemplified in Cercopidæ and in a less highly-developed state in Cicadidæ. Here Licent (1912) has done some careful work, leading him to adopt Berlese's theory for these forms also, though he found that in Cercopidæ at least there was no evidence of sugars in the liquid from the rectum; and thus he confines the action of the filter-chamber to the elimination of surplus water. Yet it is well known that the liquid excrement or honey-dew of most other Auchenorrhyncha is rich in sugars. Bates describes that of an Amazon cicada as sweetish (1863, p. 227). According to Licent the astonishing thing is that the folds of the mesenteron, in the walls of the filter-chamber, originally absorbent, reverse the action of their dialysing power and excrete the same water concurrently with the Malpighian tubules, with whose enclosed portions he found them in Cercopidæ to agree in the structure of the epithelium. Licent stresses the fact that the sap of plants is relatively innutritious—it must be taken in bulk. There is thus of necessity a rapid flow, showing itself, among other ways, in the copious evacuation of watery material from the anus in most of these forms—an evacuation at times so profuse in the case of the Cercopidæ and Cicadidæ as to lead to the belief in "rain-trees," which water the ground beneath them.

Licent believes that digestion would be difficult were there not some filtering device by which the bulk of aqueous constituents could be very quickly separated from the nutritious remainder.

To resume, the sap entering from the œsophagus is separated by osmosis in the filter-chamber into its watery constituents, which, perhaps accompanied by excess sugars, pass through the walls of the intestinal coils and straight out by the hind-intestine, and into the more nutritious matters which pass along the lumen of the stomach to enter the long and tortuous loop formed by the mesenteric sac and by the mid-intestine itself. This brings us to the function of the huge and enigmatical mesenteric sac. Note first that it lies posterior to the filter-chamber, and is thus concerned, if our theory of the latter be true, only with the more concentrated nutritious portion of the sap. Histologically, both Licent and Hickernell found it to be lined with digestive epithelium, characterized by "activité sécrétrice et absorbante," apparently not less in Cercopidæ, where it is of moderate size, than in Cicadidæ, where it is very large, and in Typhlocybidæ, where it is simply tremendous. Were it largest in Cicadidæ, one would perhaps explain such development as due to a function accessory to the auditory tympanum (mirror) as claimed by Vogel. This would then be a case slightly analogous with that of the Teleost swim-bladder, though in the Cicadidæ the sac need not necessarily have lost so completely its alimentary capacity. But its still greater evolution in the apparently silent Typhlocybids, in which, moreover, no auditory organ has yet been described, renders a predominantly gastronomic explanation more logical. That the mesenteric sac may still receive air and thus act secondarily to maintain normal air-pressure on the inner surface of the auditory tympanum is rendered probable by the fact that in Cercopid nymphs, according to Kershaw (1914, p. 65),

> "the air, which all sucking insects doubtless imbibe in quantity along with the liquid food, appears to pass through the alimentary canal and be utilized in forming the air-bubbles coated with mucinoid which are emitted from the anus and form the froth in which the nymph lives. After examining this Cercopid, I am the more inclined to believe that . . . . the 'food-reservoir' in the head of *Flata* functions in part as an air-separator to rid the liquid food of superabundant air before it passes through the alimentary canal."

Earlier (1913, p. 179) the same writer, discussing this food-reservoir after stating that its chief function, on account of its secretive activity, seems to be digestive, says :—

> "It also collects a quantity of air, separated from the food imbibed; there is always some air, often (especially just after the moult to adult) a very large amount."

This food-reservoir of the Fulgoroidea is not homologous with the mesenteric sac of the Cicadidæ and Cicadellidæ, though both pertain to the midgut. But physiologically, as in superficial appearance, they may have much in common. Granting that there is some superabundant air to be separated from the food-liquid, and supposing that this is not accomplished by the filter-chamber, then the air may be segregated, and perhaps even stored in the cicada's mesenteric sac, and serve secondarily as an adjunct to the auditory organ. In the silent nymph the sac is much less developed and considerably folded—the air may not be stored. In dissecting cicadas under water, one sometimes finds the sac to be full of gas, probably air. But such an enticing theory is to a large extent opposed by the still greater development of the sac in the Typhlocybids and other Cicadellids.

Leaving the mesenteric sac, we find that the next section of the digestive tract—the mid-intestinal loop—is, according to Licent, both absorbent and excretory. The proximal portion, up to the constriction so well marked in Cercopidæ but obscure in Cicadidæ, is almost entirely absorbent and digestive, while the part from there to the filter-chamber is excretory, like that within the latter organ. It also stores waste matter from the proximal portion. This would explain Hickernell's (1923, p. 218) observation that in *Magicicada septendecim* some sections of the ascending intestine (mid-intestinal loop) showed an epithelial lining of enormous cells filled with granules, while in others the walls were thin.

The Malpighian tubules, in so far as they enter into the filter-chamber, have been already discussed. The smooth, short, proximal portion (outside the filter-chamber), which in Cercopidæ secretes the albuminous viscid material for imparting tenacity to the foam, has not been shown to be secretory in cicada. The familiar varicose, more distal stretches perform their usual excretory functions.

The swollen excretory rectum expels the liquid waste in the forcible manner so often remarked in the Cicadidæ, particularly in European species. It is extraordinary that Hargitt (1923, p. 210) should actually state, with regard to *septendecim*, that the adults "leave no signs of excretory wastes, such as defecative products," and deduces from this that very little feeding takes place in the imaginal instar. This brings us to the subject of the next section.

e. *Feeding-habits.*

Two features of cicada life, above all others, appealed to the imagination of the ancients. One was the loud and piercing song, and the other concerned the mysterious feeding-habits. Few popular beliefs have taken so long to die as that which attributes to the cicada a diet of dew. Even Aristotle (Hist. Anim. lib. iv. cap. 7) saw nothing improbable in this "alimentum unum et peculiare." Pliny, of course, followed him, while Cardano, the physician of Milan, proved logically the nourishing properties of dew, from the fact that it was the source of the manna which sustained the Israelites in the wilderness! Hales, the English plant physiologist (1727), believed in the valuable properties of dew, which was absorbed directly by the plant.

To the question of manna produced by cicada-feeding punctures we shall return later; but here we are impelled to quote from Donovan, who was responsible for the charming English popular name applied to a Chinese cicada, namely "flea-locust." Donovan writes that cicadas "had been observed to fly among ash-trees, bore many holes in them, and when the manna had oozed out, return and carry it off."

The earliest note I have, however, of cicadas feeding on something if not more substantial, at least more nutritious, than the dew of heaven, is an observation made by Tancred Robinson in 1683-1684, but published in 1714–1716:—

> "Coming near Capua, I observ'd a Species of Ash, or *Ornus*, on the trunk whereof many Saccharin Concretions were visible. This proved the true *Manna*, that issues out thro' the Incisions made in this tree by the Inhabitants of *Calabria*. Swarms of *Cicada's* were sucking the Body and Boughs, and perhaps by wounding them made way for fresh Manna." (p. 474.)

Réaumur somewhat later (1740), describing the rostrum, says (p. x):—

> "Cette trompe apprend que la cigale n'est pas faite pour vivre uniquement de rosée;"

and instances an observation of one of his correspondents that a cicada, suddenly seized on a tree-trunk, often withdrew its mouth-parts from the bark only with great difficulty.

But the dew theory migrated to America and held sway until comparatively recent years. Potter (1839) claimed that Cicadidæ live solely on the exhalation from vegetable barks—"the insensible perspiration of the vegetable skin."

Hildreth (1830) saw the same species (*septendecim*) with its "proboscis" inserted in the bark of a tree, and a drop of liquid exuded when the mouth-parts were withdrawn.

Jaeger (1854, p. 102) retained the old fetish—"they suck with their snouts only the dew of leaves."

It is possible, although not proven, that we may have to recognize a difference, especially quantitative, in the feeding-habits of different species. Thus, in Europe, *Tibicen plebeia*, though well-known to feed (Fabre), appears to do so less frequently than *Cicada orni*, which was doubtless the subject of Tancred Robinson's observation, quoted above. In Australia, Froggatt (1903, p. 339) remarks that *Cyclochila australasiæ* does not appear to feed in the adult stage. In North America it is usually the periodical cicada which is given the palm for abstinence. With regard to this species, there were stray observations by Riley, by Davis, and by March (1889), but it was Quaintance (1902) who proved that it fed commonly, and sometimes in such numbers that the sap from the punctures was streaming down the trunks and branches of the trees.

Townsend (1892) saw *Tibicen montezuma* (Dist.) almost certainly feeding on *Yucca angustifolia.*

Gravely (1915) had a captive specimen of *Lemuriana apicalis* (Germ.) which fed on the sap of a piece of the tree on which it was caught. During feeding it emitted from time to time a jet of colourless liquid with considerable force from its hinder end.

This squirting of liquid surely is an indirect proof of feeding. We have observed it in *Melampsalta cingulata.* The fluid discharged is probably different from that emitted by the adult during the final ecdysis—a kind of moulting fluid (Davis, 1922, in *Tibicen auletes*; Krumbach, 1917, in *T. plebeia*).

The feeding evacuations are specially numerous in *Cicada orni* (Krumbach, 1917); in *Platypleura capitata* (Ol.) (*Pœcilopsaltria subfrufa* Dist.) (Biscoe, 1896) in India; and have been described in an Amazon species (Bates, 1863, p. 227). In Australia, *Psaltoda mœrens* (Germ.) feeds continually on the trunks of *Angophora lanceolata*, emitting meanwhile a spray from the anus (Froggatt, 1903, p. 340).

The most copious rain-makers are, however, reported from Mexico. Dr. W. M. Mann found that in one new irrigation district a main ditch was being constructed with an angle to avoid a rain-making tree which was considered almost as valuable as a small irrigation system, and far cheaper. An undetermined species of cicada was thickly perched on this tree, busily producing the "rain." An exactly similar tree with cicadas is recorded, likewise from Mexico, by Krieger (1904). This writer found that the evacuation was performed with a chorus effect, much like that observed in the song of the other species.

> "Beginnt eine der Cicaden ihren Tropfen zu schleudern, so ist dies das Zeichen für die ganze Gesellschaft, eingleiches zu tun, und in wenigen Sekunden ist die Erscheinung des Baumes, der nach Belieben regnen lässt, fertig."

In the case of some species, at least, it would appear that no very great restriction in feeding-habits is shown. Thus *orni*, which seems in some districts to prefer ashes and olives, in others haunts pines, and Swinton (1908, p. 380) found it in Spain feeding on especially resinous "mushroom-topped pines." He was "at liberty to pick as many of the intoxicated bridegrooms off the sticky trees as I pleased, for they had drunk the spirit of turpentine, which is a poison to Man, long and deep."

e. CIRCULATORY SYSTEM.

The dorsal vessel or heart stretches practically the entire length of the abdomen with a compartment in nearly every segment and the usual lateral muscular wings (text-fig. 71). The first or most anterior of these compartments is largest and almost circular. It is situated in the IInd segment, and sends forward the aorta, which reaches thus from the IInd segment to the head, passing between the great lateral thoracic muscle-masses. Thence it threads the foramen between the œsophageal connectives, and leads above the œsophagus to the posterior swelling of the pharynx, where it ends in an open mouth in close relation with the bases of the posterior dorsal dilator muscle of this organ.

The aorta is colourless or white, while the heart itself is dark-coloured—at least in alcohol material of *Carinata formosa.*

f. FAT-BODY.

The fat-body, representing a tissue rather than an organ, was first considered in Cicadidæ by Dufour (1825), who described it as glaucous-green in colour and most beautiful near the end of the abdominal cavity.

It is diffuse and plentiful in nymphs and in adults of both sexes, especially in the abdomen. It is permeated by tracheæ and tracheoles, and binds in sheets the intestine and Malpighian tubes. The mesenteric sac has a capacity for adhering to it wherever contact occurs, and separation is extremely difficult without rupturing the thin walls of the former.

The function of the fat-body is problematical. Comstock considers it is devoted primarily to the storage of nutriment and secondarily to excretion. It plays an interesting rôle in the cicadas and other Homoptera in supplying housing to the supposedly symbiotic Saccharomyces. According to American observers, infection by the fungus, *Massospora cicadina*, which causes such a heavy mortality among males of *septendecim*, increases with the reduction in the fat-body during adult life. Is it possible that there is an antagonism between the Saccharomyces and the *Massospora* spores? Sulc has already suggested a bactericidal function for the symbionts.

g. REPRODUCTIVE SYSTEM.

The so-called "genitalia" or appendages of the reproductive system have been treated with the chitinous skeleton generally in a previous section. This leaves us with the gonads themselves—organs with which few observers have concerned themselves. As in so many other features of internal anatomy in the Hemiptera, we turn to Dufour for the first thoroughgoing study of these organs.

Our own observations have been made chiefly upon the neotropical *Carineta formosa.*

a. Male Reproductive Organs.

Apparently the first account is that of Meckel (1808, pp. 5–7, figs. 2–5). He states that the median swollen ejaculatory duct appears to be glandular; its inner surface is beset with small openings. The figures illustrating conditions in *Tibicen (Tettigonia) plebeia* show the testes, their ducts, one pair of thick and long accessory glands, the ejaculatory duct, and the ædeagus.

Dufour (1833, p. 186, sep. pag.) deals with *Cicada orni*. He describes the general relationships with detail and accuracy. Two accessory glands were found, and considered as seminal vesicles. The ejaculatory duct is described as swollen at the base.

Berlese (1909, p. 856) copied Dufour's figure, but added little to the French author's account, which remains the best extant.

In *Carineta formosa* the two testes are roughly spherical, but at the same time diffuse (text-fig. 72, *t.*). The vas deferens from each is extremely long and complexly coiled (*vd.*). An apparently equally long and very much thicker accessory gland of unknown function opens with it into the base of the common ejaculatory duct; but just before this fusion the vas deferens and accessory gland together form a small swelling which may be considered a vesicula seminalis (*vs.*). The proximal portion of the ejaculatory duct is inordinately swollen and furnished with thick walls. Berlese names it "ampolla eiaculatrice," while Apgar (1887) mistook it for the "single testicle." Between this organ and the base of the ædeagus the ejaculatory duct (text-figs. 34, *ej.*, 72), while still strong, is of smaller calibre. It enters the ædeagus by the basal foramen.

The greatly-developed accessory glands would seem to be *mesadenia*, i. e. formed from the mesoderm, but observations on development are lacking to establish this.

Unlike the external genitalia, the gonads, especially in the male, are apparently very similar throughout the family.

β. Female Reproductive Organs.

Meckel (1808) dealt with the female as with the male gonads in *Tibicen plebeia*. He was the first to describe the single long, thick, unpaired, accessory gland opening near the aperture of the vagina at the base of the ovipositor. He states that this gland arises from a swelling which gives rise to two tubes, one the neck of the spermatheca and the other the common oviduct. The latter branches into two pairs of canals—one those of the paired accessory glands and the other the oviducts. The paired glands seem to contain the same matter as the unpaired.

Dufour gave a detailed description in 1825, recognizing two long vessels secreting "sebaceous humour." The whole account was modified in 1833, and, among other matters, three of these vessels were shown. They are described as being half as long as the insect, membranous, semi-diaphanous. Their positions are

e. CIRCULATORY SYSTEM.

The dorsal vessel or heart stretches practically the entire length of the abdomen with a compartment in nearly every segment and the usual lateral muscular wings (text-fig. 71). The first or most anterior of these compartments is largest and almost circular. It is situated in the IInd segment, and sends forward the aorta, which reaches thus from the IInd segment to the head, passing between the great lateral thoracic muscle-masses. Thence it threads the foramen between the œsophageal connectives, and leads above the œsophagus to the posterior swelling of the pharynx, where it ends in an open mouth in close relation with the bases of the posterior dorsal dilator muscle of this organ.

The aorta is colourless or white. while the heart itself is dark-coloured—at least in alcohol material of *Carinata formosa*.

f. FAT-BODY.

The fat-body, representing a tissue rather than an organ, was first considered in Cicadidæ by Dufour (1825), who described it as glaucous-green in colour and most beautiful near the end of the abdominal cavity.

It is diffuse and plentiful in nymphs and in adults of both sexes, especially in the abdomen. It is permeated by tracheæ and tracheoles, and binds in sheets the intestine and Malpighian tubes. The mesenteric sac has a capacity for adhering to it wherever contact occurs, and separation is extremely difficult without rupturing the thin walls of the former.

The function of the fat-body is problematical. Comstock considers it is devoted primarily to the storage of nutriment and secondarily to excretion. It plays an interesting rôle in the cicadas and other Homoptera in supplying housing to the supposedly symbiotic Saccharomyces. According to American observers, infection by the fungus, *Massospora cicadina*, which causes such a heavy mortality among males of *septendecim*, increases with the reduction in the fat-body during adult life. Is it possible that there is an antagonism between the Saccharomyces and the *Massospora* spores? Sulc has already suggested a bactericidal function for the symbionts.

g. REPRODUCTIVE SYSTEM.

The so-called "genitalia" or appendages of the reproductive system have been treated with the chitinous skeleton generally in a previous section. This leaves us with the gonads themselves—organs with which few observers have concerned themselves. As in so many other features of internal anatomy in the Hemiptera, we turn to Dufour for the first thoroughgoing study of these organs.

Our own observations have been made chiefly upon the neotropical *Carineta formosa*.

α. *Male Reproductive Organs.*

Apparently the first account is that of Meckel (1808, pp. 5-7, figs. 2–5). He states that the median swollen ejaculatory duct appears to be glandular; its inner surface is beset with small openings. The figures illustrating conditions in *Tibicen* (*Tettigonia*) *plebeia* show the testes, their ducts, one pair of thick and long accessory glands, the ejaculatory duct, and the ædeagus.

Dufour (1833, p. 186, sep. pag.) deals with *Cicada orni*. He describes the general relationships with detail and accuracy. Two accessory glands were found, and considered as seminal vesicles. The ejaculatory duct is described as swollen at the base.

Berlese (1909, p. 856) copied Dufour's figure, but added little to the French author's account, which remains the best extant.

In *Carineta formosa* the two testes are roughly spherical, but at the same time diffuse (text-fig. 72, *t.*). The vas deferens from each is extremely long and complexly coiled (*vd.*). An apparently equally long and very much thicker accessory gland of unknown function opens with it into the base of the common ejaculatory duct; but just before this fusion the vas deferens and accessory gland together form a small swelling which may be considered a vesicula seminalis (*vs.*). The proximal portion of the ejaculatory duct is inordinately swollen and furnished with thick walls. Berlese names it "ampolla eiaculatrice," while Apgar (1887) mistook it for the "single testicle." Between this organ and the base of the ædeagus the ejaculatory duct (text-figs. 34, *ej.*, 72), while still strong, is of smaller calibre. It enters the ædeagus by the basal foramen.

The greatly-developed accessory glands would seem to be *mesadenia*, i.e. formed from the mesoderm, but observations on development are lacking to establish this.

Unlike the external genitalia, the gonads, especially in the male, are apparently very similar throughout the family.

β. *Female Reproductive Organs.*

Meckel (1808) dealt with the female as with the male gonads in *Tibicen plebeia*. He was the first to describe the single long, thick, unpaired, accessory gland opening near the aperture of the vagina at the base of the ovipositor. He states that this gland arises from a swelling which gives rise to two tubes, one the neck of the spermatheca and the other the common oviduct. The latter branches into two pairs of canals—one those of the paired accessory glands and the other the oviducts. The paired glands seem to contain the same matter as the unpaired.

Dufour gave a detailed description in 1825, recognizing two long vessels secreting "sebaceous humour." The whole account was modified in 1833, and, among other matters, three of these vessels were shown. They are described as being half as long as the insect, membranous, semi-diaphanous. Their positions are as observed by Meckel. In the figure (188) the spermatheca is labelled as the reservoir of the sebaceous gland.

Doyère (1837 *b*) studied the parts immediately adjacent to the base of the ovipositor in great detail, in *Cicada mannifera* (Fabr.). (=*Fidicina m.*). He described what he believed to occur during copulation, stating that the penis proper finds its way into the diverticulum, which he called *poche copulatrice*. He discovered the small vesicles on the neck of the latter and the long filiform tubes which Gadd (1910) thought had escaped all previous eyes. Doyère noticed that these vesicles contained a fatty substance of a yellow colour, evidently secreted by the hair-like tubes. He found the tubes themselves to be five to ten times as long as the body, and confirmed the presence in this third species of the three stouter accessory glands of Meckel and of Dufour (1833).

Holmgren (1899) used Cicadellids, Cercopids, and one Fulgorid in his investigations of the female reproductive system, but made a comparison with Doyère's and with Dufour's results. The chief point of difference appeared to be the lack of the paired accessory glands opening at the junction of the oviducts.

Henneguy (1904, p. 166) remarks that the *poche copulatrice* receives the semen in Cicadidæ, and this is then stored in the receptacula seminis, of which the cicadas possess two (p. 169). This is surely an error, unless the latter name is applied to the small vesicles on the neck of the bursa.

Berlese (1909) fails to mention the unpaired accessory gland, but otherwise follows Dufour closely.

Gadd (1910) studied the female reproductive system in *Tibicen plebeia*, *Cicada orni*, *Cicadatra querula*, *C. atra*, *C. hyalina*, *Melampsalta adusta*, and *M. montana*—seven species in all. In all he found the unpaired gland first described by Meckel, and noticed that in *plebeia* and *orni* it is very long, reaching to 20 mm. in the former, while in *Cicadatra* it is reduced, and in *Melampsalta* much shorter than the oviduct. This may therefore explain my own failure to find it in *Melampsalta* and in *Carineta*. Similarly, the efferent canal of the receptaculum seminis in both *Cicadatra* and *Melampsalta* (*Cicadetta*) is proportionately shorter than in *orni* and in *plebeia*. Gadd claims the discovery of the paired filiform glands opening into vesicles at the entrance of the *receptaculum seminis*. We have seen, however, that these were accurately described by Doyère in 1837. Gadd's *receptaculum seminis* is evidently our apical pouch (text-fig. 75, *ap.*).

In *Carineta* there are, as in other species known, two large ovoid ovaries (text-fig. 73, *ov.*). These contain in a European species 70–80 meroistic ovarioles, according to Berlese. The number in *Carineta* seems to be of the same order.

The oviduct (text-figs. 73, *o.*) bends shortly and runs to join its fellow and form a stout, short, common oviduct or vagina (text-figs. 73–75, *co.*). This bends over very sharply near its beginning, and just after the union of the oviducts receives a long, winding, accessory gland from each side. These appear homologous with the very similar structures in the male, but are shorter. They can, of course, be considered neither spermathecal nor colleterial glands, and their function remains for the present unknown.

Near the external opening the vagina receives a large sac-like spermatheca. Comstock (1925, p. 160) remarks that a *bursa copulatrix* is said to be wanting in Hymenoptera, Diptera, Heteroptera, and Homoptera, except the Cicadas. I am not clear to which organ in the cicadas Comstock would apply this term. There is only one large sac-like appendage to the vagina in this and in other recorded species. This appendage, the spermatheca, shows, however, a differentiation very marked, into a relatively soft-walled apical pouch (*ap.*) and a very stout and muscular portion proximally (*ms.*). Possibly the latter subserves the function of bursa copulatrix, but we are here calling the whole organ a spermatheca.

At each side of the entrance of the spermatheca (or bursa, Comstock) is a tiny thin-walled sac receiving a long, much coiled, thin, and thread-like white gland discovered in other species by Gadd in 1910 (text-figs. 73–75, *acs.*). These glands, which are cut short in our figures, are to be considered as spermathecal glands.

Finally, as to the large, very long, unpaired gland opening into the vagina near its orifice, as discovered by Dufour and confirmed by Gadd (1910), but omitted by Berlese (1909, fig. 1132) from his copy of Dufour's figure, I have found traces neither in *Carineta formosa* nor in *Melampsalta scutellaris*; but the condition and quantity of my material hardly warrant the assumption that it is therefore absent in these species. Gadd found it very short in *Melampsalta adusta*.

In *Melampsalta scutellaris* the filiform spermathecal glands are thicker and somewhat shorter than in *Carineta*. The vesicle on each side, into which each opens, is larger than in the other genus, translucent and bright yellowish-green instead of white as in *Carineta*.

(3) SOUND-ORGANS.

We now come to those parts of cicada anatomy which, above all others, have enabled these insects, in more senses than one, to make a noise in the world. We have here to deal with the most complicated sound-producing organ in the animal kingdom—and one which usurps such a large part of the cicada economy as to remind us forcibly of Plato's story that these insects were once men who gave up their whole lives to song, neither eating nor drinking, and singing, died.

The following comprises, firstly, a description of these organs as they occur in *Melampsalta*, notes on their mechanism and a discussion of the further specialisation exhibited by the Platypleurinæ, and a few notes on the condition of the corresponding parts in females and nymphs; secondly, a historical review of our knowledge of cicada sound-organs; and, thirdly, an account of the accessory stridulating apparatus of the subfamily Tettigadinæ. It has been necessary to depart from historical sequence in this arrangement, since a description of the organs is a pre-requisite to a just evaluation of earlier contributions to their morphology.

a. DESCRIPTION OF SOUND-ORGANS. (Text-figs. 10, 14, 16–23, 27–29.)

Unless otherwise stated, the description is based on New Zealand species of *Melampsalta*, chiefly *sericea* and *muta*. An effort has been made to stabilize the terminology.

1. The *opercula* are two large plates on the underside of the body, extending posteriorly from the metathorax and covering a large ventral cavity. In *Melampsalta* they are short, in *Lembeja* (*fatiloqua*) and in *Tettigarcta* entirely absent, but in some species of the Oriental Dundubiini—in many respects the most highly specialized of all cicadas—they are extraordinarily elongated and attain nearly the apex of the abdomen. Text-fig. 10, if nothing else, shows that these organs are extensions of the metathoracic epimera, as stated by Carlet. Mayer (1877) and Prochnow (1907–8) consider them *episternites*. Comstock calls them outgrowths of the sternella, but in *septendecim* they may be seen distinctly to curve round the metasternum, which itself bears a projection (apophysis of Carlet) for the insertion of the folded membrane. The opercula are the *volets* of Réaumur, Carlet, and Fabre. They have been inexcusably mistaken for the agents of sound by several taxonomic writers; thus Francis Walker calls them the *drums*, and applies the term *opercula* to the lateral coverings of the tymbals in Platypleurinæ.

Projecting over the base of each operculum is a meracanthus which Réaumur (*cheville*) believed to function as a lock to prevent the operculum from moving too far from the plane of the abdomen. But the operculum is immovably attached to the thorax, and the space between it and the abdomen, which in some species is varied during singing, is altered by lifting the abdomen from the operculum. The effect, of course, is the same. The opercula are moderately developed in the female.

2. The *cavity*—the *church* or *la gleiso* of the Provençal peasant—lies beneath the opercula. It is bounded anteriorly on each side by a yellowish *folded membrane*, which is apparently the intersegmental membrane between the thorax and abdomen, and posteriorly by a *mirror*, which has already been described as the tympanum of the chordotonal organ lying in the lateral wall of each IInd abdominal segment. The mirror has usually been considered (*e.g.* by Mayer, 1877) as the intersegmental membrane between the Ist and IInd abdominal segments, but Vogel, as we shall see later, sees in it the "*Pleuralhaut*" of segment I. Apart from the opercula, the mirrors are the only organs of this

complex which are present in the female. The folded membrane is probably only of articulatory importance; but Carlet describes a small tensor muscle, and believes the membrane is an accessory vibratory structure, a character assigned also, by assumption, to the mirrors until they were recognized as the tympana of the auditory organs. Vogel describes also (1923, Abb. 5) a tensor muscle of the mirror, but I have been unable to find any trace of this in *Melampsalta* (text-fig. 27).

3. The spiracles associated, in our opinion only topographically, in that of other observers (Carus, Landois, Swinton) functionally, with the sound-organs are the third and fourth pair (first and second abdominal). Their position has already been described in section (2) *c*. of the present paper. We have seen also that the *tracheal sac* of many observers is mesenteric in origin and has no communication yet proven with the spiracles. Some writers, concerned only with the sound-organs and dissecting probably dried material, have not even recognized a sac, but speak of the third spiracle as opening directly into the body-cavity (Carlet, 1877, p. 20, in *Tibicen plebeia*). Vogel claims that the wall of the sac is fused with the tympanum, the two together forming a wall only 0·5 μ thick!

4. We have reserved till last the effective instrument of sound. All the foregoing structures are mostly protective and accessory. The sides of the Ist abdominal segment show as tergal modifications two convex, oval, strongly-chitinized, pale-coloured plates in a frame even more stoutly chitinized. In *Melampsalta* the surface of each *tymbal* shows usually a posterior smoother portion with one strong rib at its edge and an anterior with strong, more or less parallel ribs, slightly oblique but not far from perpendicular to the long axis of the cicada body. These ribs are darker in colour than the rest of the tymbal. In *Magicicada* there is a greater development of parallel ridges and less smooth space. The tymbal of *Tibicen chloromera* is more like that of *Melampsalta*.

5. Dissection is necessary to lay bare the musculature which puts these organs in motion (text-fig. 28). It is convenient to cut off the abdomen at about the IIIrd segment. In caudal view the mirrors are then very conspicuous, and the other organs may be seen through them. Prominent among the latter is a large chitinous V, standing on the sternal surface and reaching its arms up almost to the dorsum. This is the *triangle écailleux* of Réaumur and the *entogastre* of Audouin and Carlet. The whole or part of this structure has been homologised incorrectly as the furca of an abdominal segment, interpreted either as I. or II. We shall consider its true nature in the sequel.

Parallel but dorsal to the arms of the V, and inserted in a ridge in the basal portion of each, are two large muscles—the largest single muscles in the body. These are the tymbal-muscles. Each bundle ends distally in a chitinous plate—*Sehnenplatte* of Vogel, *plaque cartilagineuse* of Réaumur, *épidème* of Audouin, *disque terminal* of Carlet,—from which a narrow tendon extends to its attachment in the dorsal portion of the inner face of the tymbal at the main ridge of the smoother portion (text-fig. 28).

Tymbal-covers.—We have described the complete sound-producing apparatus as it appears in its simplest form. In the Platypleurinæ, to which subfamily belongs *Tibicen plebeia*, the species most often studied by European workers, the tymbals are completely hidden from view by a forward lateral expansion of the second abdominal tergite, which forms on each side an accessory cavity of which the inner wall is formed partly by the tymbal. These second cavities—*cellules* of Réaumur, *cavernes* of Dugès—are much narrower but considerably deeper than the main one bounded by the opercula, folded membranes, and mirrors. In the subfamily Cicadinæ (Gæaninæ Dist.) the tymbal covers are incomplete.

The essential elements of the sound-producing apparatus are the tymbals and the tymbal-muscles. The experiments of Laurentus (Zanotti, 1731, p. 80), of Lepori (1869), of Mayer (1877), of Solier (1837), of Goureau (1838), of Medici (1847), of Lucas (1887), to mention only a few, all attest the fact that the destruction of actual or supposed accessory parts—opercula, folded membranes, mirrors, "tracheal" sac—and the stoppage of the adjacent spiracles have but the slightest, if any, quantitative effect on the production of sound in the living cicada. Landois's theory that the third spiracles were the instruments of sound never had the slightest experimental foundation, but, on the other hand, went against all previous evidence. The more reasonable belief of Carus and others that the spiracles acted as accessories by supplying the air to the "tracheal" sac was based on observations made on *Tibicen plebeia* while singing. This species, like several of the New Zealand Melampsaltæ, modulates the sound by alternately widening and narrowing the entrance to the main cavity by raising or lowering the abdomen. This rhythmical movement was mistaken by Carus for a respiratory one. In those species, like *Melampsalta muta* in New Zealand, which do not thus manipulate the opening while singing the song is uniform and monotonous, though the volume of sound is no smaller.

We are reduced, then, to the tymbals and their muscles. The former are convex, and if they are pulled inward and released by manipulation of the appropriate muscles in a moist specimen, they will regain their former convexity by virtue of the elasticity which resides especially in the strongly-bowed ribs. This process is accompanied by a short click like that emitted by a tin can similarly indented—and these clicks, rapidly repeated, constitute the song of the cicada. No further arrangement is required. But the simplicity of this explanation, first clearly demonstrated, though not discovered, by Réaumur, has been repugnant to several investigators, and Graber would see in the sound a result of friction between the ribs of the tymbal during the alternate movements of contraction and relaxation. Hingston (1922) carries this idea still further—believes that the click elicited by manipulation of the apparatus in a dead cicada results from the tapping of a tooth borne by one of the ribs on a bar which corresponds with another thickening. Since the tymbal structure necessary for this method is far from general in the family, and may be even confined to the one species studied by Hingston, this explanation, even if partially true, is too limited to apply to cicada music as a whole. So far as we can see, in a dead specimen of *Tibicen chloromera* the movement of the tymbal is just a simple buckling on a line near the middles of the chitinous bars, and almost parallel with the long axis of the body.

Carlet attempted (1877) to measure the vibrations of the tymbal by fixing a fine glass thread with wax to this organ and placing the other end of the fibre in contact with a revolving cylinder furnished with a smoked surface. The experiment was not very successful, largely because a captive cicada never sings "properly," but emits an alarm cry like that of a bird under similar circumstances.

The same observer (1876 *b*) observed that the tymbal-muscles contract simultaneously.

It is needless to state that the sound-organs are confined entirely to the males. Apparently Amyot (1836) was the first to make the statement that certain unspecified exotic forms had the sound-organs almost as well developed in the male as in the females, and that presumably these females sang too. Although this seems to be entirely incorrect, it has been repeated in several reputable works, even as recently as 1909 (Berlese). Girard (1866) states the belief very dogmatically.

Homologies of the Sound-organs.—The interpretations offered towards the solution of the homology of the structures involved in the sound-producing apparatus are confusedly various. The following points are, however, agreed upon by almost all workers :—

a. The tymbals are modified portions of the first abdominal tergite.

b. The tymbal-covers in the Platypleurinæ are outgrowths of the IInd segment of the abdomen.

c. The folded membrane is the modified intersegmental membrane between the metasternum and the ventral part of the abdominal base.

It may be further taken as established, in spite of assertions to the contrary, that the following homology is substantially correct :—

a. The opercula are productions of the metathoracic *epimera* only.

b. The mesenteric (so-called "tracheal") sac is primarily a part of the alimentary tract.

The most important of the remaining questions concern the origin of the furca-like structure supporting the tymbal-muscles, and of the mirrors or auditory tympana fastened along one of its edges. In the solution of these problems it is possible that a dissection of *Tettigarcta*, which is devoid of sound-organs, would be of assistance. Scarcity of material makes this impossible at present, but an external examination shows the following conditions in the adult male:—The opercula are completely lacking; there are not even the rudiments seen in the females of other species. The Ist abdominal segment is greatly reduced, but shows laterally a slightly swollen area, free from the long hairs which thickly clothe the rest of this region, and furnished with faint ridges. Were not nearly all the other characters of *Tettigarcta* apparently highly primitive, one would be inclined to see in this structure the last vestiges of tymbals lost in the history of the race. There are no signs of a mirror.

Berlese considers the chitinous V in question to be the furca of the second abdominal sternite (p. 707) or of the first (fig. 633) —an inconsistency not unusual in the Italian worker's great book. Comstock (1925) agrees with the first homology, while Imms (1925) states that the tymbal-muscles arise from the "mesofurca." The two authors, however, who have given the matter the most attention are Carlet (1877) and Vogel (1923). The former sees in the structure in question an endoskeletal development of the Ist abdominal segment, and calls it the *entogastre*, while Vogel likewise ascribes it to segment I., a conclusion which, as we shall see, there can be no disputing.

All previous workers have studied the homologies of the sound-organs only in adult males, with an occasional glance at a female. but we have attempted to follow a developmental series, beginning with a female nymph, as likely to contain the least rudiments of the apparatus, then studying the male nymph, the adult female, and then the adult male. This has been done with those species of which we have authentic material of the pre-imaginal stages—namely *Melampsalta leptomera*, *M. serica* and *M. cingulata*, and *Magicicada septendecim*.

1. The female ultimate nymph shows the first sternite greatly reduced—in fact almost obsolete. Internally there is a powerful furca from the metasternum, but not the slightest trace of endoskeletal structure in abdominal segments I. and II. (text-fig. 22).

2. The male ultimate nymph shows surprisingly little difference from the female condition. There is, however, a raised dome-like area of smooth, white, very thin skin where the tymbal will lie on the Ist abdominal segment. This is so large as to suggest that the adult organ owes its structure and strength largely to excessive folding of this area. The rudiment of the hearing-capsule is more swollen than in the female. The

boundary between segments I. and II. is rather indistinct, and, apart from the auditory capsule, very membranous. *There is no more trace of abdominal furcæ here than in the female of corresponding age*, while those of the thorax are distinct and well developed.

3. In the adult female (text-fig. 20) the nymphal conditions have been much modified, especially in abdominal segments I. and II. The chitinized part of the 1st sternite (text-fig. 14) is very small. The mirror has come into being, but is much smaller than in the male. Its front border is formed by a narrow chitinized piece. Its hind-border arises distinctly from the 1st sternite as a chitinous strip which, as seen from within, runs into the 2nd sternite and seems to be continuous with the posterior margin of a flap folded back on the 2nd sternite (text-fig. 20, *fl.*), along the intersegmental line. The lower margin of the mirror is attached to the posterior edge of this flap. We shall see later whether the flap itself belongs really to I. or II., but the fact is assured that the mirror lies wholly in segment I., and consists of a thinning of the sternite itself, as Vogel (1923) was apparently the first to recognize. Moreover, the line separating I. from II. passes between the 4th spiracle and the auditory capsule, and the former must therefore be considered as topographically belonging to I. There is no spiracle actually situated on segment II. If Heymons and others who believe there is a forward shift of spiracles during development in this region are correct, then spiracle 3 belongs to abdominal segment I., but has moved on to the posterior edge of the metathorax, while spiracle 4 has made a similar shift from II. to I. If, on the other hand (see section (2) *c.* of this paper), these workers are wrong, and spiracle 3 belongs truly to the thorax, as its structure would seem to suggest, we are faced, whether 4 belongs primitively to I. or II., with the anomalous conclusion that a spiracle occupying an intermediate position in the series has been lost entirely. We prefer the former explanation. Vogel believes that the line separating the mesal border of the mirror from the chitinized mesal part of sternum 1 is homologous with Heymons's embryonic division between sternite and parasternite. Thus the mirrors would correspond with the parasternites of segment I. The validity of this division as applied to adult structure is, however, very questionable (see section (1) *c.* of this paper), and we prefer to regard the auditory tympanum merely as a differentiated part of sternite I. without committing ourselves to its homology with a more or less hypothetical parasternal segregate.

There is no sign of endoskeletal structure in the female abdominal segments I. and II.

Turning now to the adult male (text-fig. 19), we can understand the position better by comparision with the female. The small strongly-chitinized 1st sternite of the female is here merely bent more sharply upward on each side, and continued into the fore-rim of the mirror in accordance with the much greater development of this organ. In the male this fore-border is much wider, stronger, and more wing-like (text-fig. 29), and extends, as in the female, to the neighbourhood of stigma 4 and of the lower corner of the tymbal—*i. e.* to tergite I. Thus this wing-like fore-border is really part of the outer body-wall of the 1st segment, and, in fact, merely a differentiated part of sternite I. There is nothing really endoskeletal about it—yet it is an arm of the V which has been called the furca of the IInd sternite. A glance at text-fig. 29 will show that it belongs entirely to segment I.—the line of demarcation is clear. Anterior to this differentiated part of sternite I. on each side lies the folded membrane, and posteriorly the mirror. If we accept the parasternite conception, then this wing is part of parasternite I. along with the mirror. All that has happened is that the entire latero-ventral portions of sternite I. have been strongly constricted—pushed dorso-mesally, so as to leave a resonatory cavity between what is really the ventral surface of segment I. and the opercula, which lie in the normal plane of the venter. No endoskeletal structure has been produced since the whole of segment I. has participated in the change. The tergite has supplied the tymbal on each side, while the sternite has differentiated in each lateral region into a strong chitinous anterior portion serving as a support for the greatly thinned posterior part or mirror. Text-fig. 29 shows that there is a slight inward buckling near the base of the two sternal wings in *septendecim.* The two parallel ridges formed thus, one on each side, tend to approximate each other. They are the nearest approach to endoskeletal structure found in this segment, and they serve as the fixed insertion of the tymbal-muscles. In *Tibicen chloromera* these ridges are better developed and practically meet, forming a strong carina performing the same function.

The hind edge of the mirror is formed, as in the female, by a strongly-chitinized flap apparently from the 1st sternite, folding over within the anterior edge of the 2nd sternite, thus making a strong reinforced rim. Whether this flap itself (text-fig. 20), curving backward and inward over the edge of the 2nd sternite, belongs to segment II. or to segment I. is difficult to decide. The 1st segment separates easily from the IInd along the intersegmental line in KOH preparations, and the tear always continues right along this fold, thus separating the flap in question from segment II. But along the fold there is no sign of a real suture (text-fig. 21), and, moreover, the posterior sternal wings (text-fig. 29) are not continuous with the flap, as viewed from within. At the lateral or dorsal extremity of the fold, on the other hand, the chitin *is* continuous.

This question, however, does not affect the conclusion that the whole of the sound-producing apparatus, together with the tympana of the chordotonal organs, belongs to abdominal segment I.

To the homologies already tabulated at the beginning of this subsection we should therefore like to add the following:—

a. The wings of the so-called *furca* (Berlese, 1909, figs. 433, 882) supporting the tymbal-muscles at their base are not endoskeletal, but are differentiated anterior parts of the 1st sternite.

b. The mirrors or tympana are differentiated posterior portions of the 1st sternite.

c. The whole of the sound-organs pertains to segment I.

b. HISTORICAL REVIEW.

The first known observation on the method of sound-production in the Cicadidæ—that of Hesiod, about the eighth century before Christ—we have seen to be accurate so far as it goes. The tettix "pours forth *from under his wings* his shrill song."

Aristotle's much later and more detailed account, an extension, so far as the scientific equipment of the time would allow, of Hesiod's observation, was the first attempt at a formal explanation. We must examine it a little closer. The relevant passages (Hist. Anim., lib. iv. cap. 9; De part. anim., lib. iii. cap. 16), though short, have given considerable trouble to the commentators The following interpretation is based on the various editions and commentaries cited in the bibliography, and on the exegetical notes of Landois (1867). The explanation involves Aristotle's conception of respiration, which he regarded as essentially a process of cooling. Vertebrates accomplish this result by taking air into the body and expelling it again. Insects do not breathe in this sense, but achieve the same end by the agitation of the air enclosed within their bodies. By this movement the body fluids are brought into contact at the *hyposoma* with the thin membrane which there separates them from the cooler outer air. Ogle and Landois think that the *hyposoma* is the waist-line or septum between thorax and abdomen in its ventral part. In flies, bees, and similar buzzing insects this sound is produced by the vibration of the membrane at the *hyposoma*, brought about "*attritu spiritus*." In those tettiges which sing, the hyposomatic insinking is much more greatly developed, but the song is produced in the same way. Landois compares the agitation of the "innate spirit" (Ogle) with the movement we might impart to the air in our chest by moving our diaphragm up and down while keeping the nostrils and lips closed. We do not think Ogle's above translation for πνεῦμα is well-advised, for Aristotle apparently meant the term to connote merely enclosed air without any metaphysical implications. The movement was conceived as produced by relative motions of the internal organs.

Such was the explanation which held sway until after the Renaissance. It possessed the merit of distinguishing clearly between the song of the cicadas and the stridulation of Orthopteroids; and it was as definite as the biological concepts and scientific equipment of the time would allow. The absence of even the rudiments of knowledge concerning muscular action on the one hand and respiration on the other, in invertebrates, made it impossible to distinguish in principle the song of the cicadas and the buzzing of bees and flies.

The two other main theories of cicada sound-production advanced in classical times are superficial in comparison. On the one hand, Meleager, Apollonides (or Philippus), and other writers in the Greek Anthology, by confusion with Orthopteroid stridulation, spoke of such methods as "beating its belly with its wings," "striking its feet with its wings," or its body. On the other hand, was the idea, apparently Egyptian, though mentioned also by Bianor in the Greek Anthology, that the rostrum, rubbing on the under surface, was the plectral instrument of sound (Horapollo, Valeriano).

But these superficial notions competed little with the Aristotelian hypotheses, which was repeated by mediæval and later writers down to Aldrovandi (1618) and Moufet (1634), and constituted, from the scholastic viewpoint, a perfect explanation, requiring only abstention from renewed investigation to ensure its indefinite perpetuation. The one glimmer of experimentalism —the observation of Albertus Magnus (published 1495) that cicadas could sing for a considerable period after decapitation—served only to confirm the theory.

The first to dispute, in the opening of the seventeenth century, the authority "che per tant' anni avea celato il vero," were Casserius and Galileo. Galileo's statement is a clear expression of the modern spirit and a clean sweep of tradition, but at its publication the effective organs of cicada sound had been already discovered by his contemporary. Giulio Casserio (Casserius), erstwhile domestic in the household of Fabricius ab Aquapendente and later his successor in the Chair of Anatomy and Physics at Padua, published in 1600 a detailed illustrated account of several species, figuring the tymbals (*membranæ bracteales*), mirrors (*tympana*), folded membrane (*membranæ luteæ*), and tymbal-muscles, which latter he described as "*ad mouendas membranas effecti.*" The relations of the muscles are clearly shown, save that the terminal disc and tendon are omitted and the muscle drawn as inserted directly on the tymbal by a slightly narrowed apex. There is, however, some mistake in his experiment, since he remarks concerning the folded membrane (*membrana lutea*) "*disrupta sonus perit.*" Considering the time at which he wrote, and the more than a century's interval which passed before his studies received a worthy supplement, the contribution of Casserius is highly noteworthy. His work, published in a general anatomical treatise, seems largely to have been overlooked by his successors.

The next account, that of the Spanish botanist Giulio Pontedera (1718), falls considerably short of the standard set by Casserius so long before. It is true that he promises a fuller and illustrated description, but this apparently never appeared. He indeed recognized the tymbals, and observed that the sound ceased when they were broken. His outlook was predominantly traditional, however, and he appeared still to believe that the tymbals were moved by the air enclosed in the body, but his account is so obscure that one follows his thinking with difficulty.

Giovambatista Felici is credited by Medici (1847, p. 142) with publishing the first figures of the sound-organs (1724), but we have seen that another Italian, Casserio, has no fewer than 124 years' priority. But if that honour go to Casserio, nevertheless the standard of Felici's work makes him a worthy second.

Felici's investigations were said to have been made and communicated in 1717, seven years before publication. Felici held a generally correct view as to the relations of all the parts; he discovered the terminal plates of the tymbal-muscles, *ossetti o cartilagini dure*, and the tendons connecting them with the inner face of the tymbal. He knew no previous theories save those of antiquity, and these he criticised soundly, characterising the Aristotelian conception as a well-thought-out hypothesis—

> "Ma quanto (o Dio!) agevolmente s'ingannano coloro, che per investigare le cagioni degli effetti naturali, non hanno altra migliore scorta che la propria fantasia!" (1724, p. 67.)

By experiment he showed that the mirror and other necessary parts—one by one—could be eliminated as sound-producers, until finally he could demonstrate this rôle in the tymbals alone.

Felici figures and names five different species of true cicadas.

Zanotti (1731) records the investigations of Pozzi (Putius) and Laurenti, carried on some ten years previously. Those of Laurenti were devoted to the sound-organs. Zanotti refers to Felici's work, and fails to show that Laurenti adds anything to the latter's contribution. The tymbals are described, and the now almost usual experiment performed to show that their extirpation renders the animal mute. The tymbal-muscles are not, however, mentioned.

Swammerdam (1737, p. 504) knew no cicadas in nature: we may therefore excuse his repetition of the Aristotelian explanation.

Four times at least now had the true sound-organs been independently discovered and their mechanism more or less clearly described. It is significant that the poorest account of the four was that of the investigator who placed the most emphasis on the teaching of the classics. To the extent that these isolated experimenters broke away from traditionalism, to that extent also did they tend to ignore the work of their contemporaries and immediate predecessors. In no one were both tendencies more clearly displayed than in the fifth independent discoverer of cicada sound-organs. But it was due to the unfailing accuracy and patience of his observations, to the clarity and detail of his illustrations, and to the lucidity and charm of his literary style that Réaumur (1740) not only escaped the oblivion which has largely swallowed the work of his forerunners, but supplied the account which is the basis of nearly all subsequent *accurate* descriptions of these organs. Even Fabre considered that the "master" had cleared up most of the mystery, leaving only a few supplementary facts for his disciples to glean.

Fabre is right—those who, like Landois (1867, 1874), loudly proclaim that, instead of adding a little to the work of their predecessors, they have reaped an entirely new harvest, are found usually to have stored nothing but chaff. Réaumur's account, remarkable for its uncompromising denial of any other motor agent than that furnished by the tymbal-muscles, is too well-known, at least by imitation and abridgment, to require further comment.

Later workers who, while adhering to the essence of the Réaumurian interpretation, have in many cases added greatly to our detailed knowledge of cicada sound-organs are Carlet (1876 *a*, 1876 *b*, 1877, 1879), who has perhaps given the best general account; Fabre; Haswell (1887); Lucas (1887); Mayer (1877); Lepori (1869); Goureau (1837, 1838); Targioni (1867); Medici (1847); Latreille (1822); Middlemiss (1886); Hingston (1922); Dugès (1838); Graber (1872, 1876, 1877); N. Potter (1839); Lloyd Morgan (1880, 1886).

Lepori and Goureau showed that the stigmata had nothing to do with the sound, since it was not altered when these were blocked.

Carus (1829) emphasised very strongly an alleged respiratory factor mentioned by Chabrier (1820), but which Carus claimed that Réaumur and his disciples had overlooked. He observed *Tibicen plebeia* in Italy. Now *plebeia* is one of those species, like *Melampsalta scutellaris* in New Zealand, which "play" their instruments with considerable ingenuity, modifying the sound by alternately lifting the abdomen from and appressing it to the opercula, and thus varying the size of the entrance to the sound-organ cavity. At its greatest divergence the abdomen is slightly curved dorsad of the usual outline of the body, and appears swollen. The whole process looks very like a swelling and deflating of the abdomen itself. Hingston (1922) describes it as an actual operation of this kind—the abdomen in a Himalayan species was seen to distend and collapse in accordance with increase and diminution of pitch in the song. Yet a hole cut in the side of the abdomen and of the mesenteric sac failed to stop the song. Carus, however, believes that the movements were distinctly respiratory, and accompanied the alternate expiration and inspiration of air through the third spiracles. He regarded this process as *per se* essential to sound-production, and knew nothing of the alternate increase and decrease of the space between opercula and venter. In this interpretation he was followed by Burmeister (1833); van Hasselt (1882); Milde (1886); and, in independent agreement, by Solier (1837). We have seen that Lepori, Goureau, and Hingston have supplied refutation based on experiment, while we have interpreted with Fabre, Swinton (1880, p. 222), and others the effect of the movements in another way. Swinton (especially 1908) would seem to believe, nevertheless, that the movements are respiratory.

There remain four theories which are now little more than historico-scientific curiosities. Griffini (1897) writes (p. 570) of cicadas:—

> "Le loro elitre hanno le nervatura basali vesicolose, ossia alte a dilatarsi ed a deprimersi alternativamente."

This alternate swelling and deflating of the "nervatura" produces cicada song!

Bartram (1894) claims that the males of *Magicicada septendecim* make a noise "by a tremendous motion of two air-bladders under their wings." His countryman Hildreth (1826), by a happy thought, extends this hypothesis to explain also the origin of the Scottish national musical instrument. He refers to *septendecim* as "screaming with their air-bladders or bagpipes" placed under their wings, and suspects that the inventor of bagpipes received the idea "from some insect of this kind"—surely a Southron origin for the pipes. Possibly Hildreth was influenced by the question as to the musical properties of either instrument.

Rosel (1749) suffered with Réaumur, whose work he knew well, the disadvantage of working with dead material. But while the French naturalist's cicadas were preserved in alcohol, the Nuremberg observer had apparently only dried specimens. He found that the tendon from the terminal plate of the tymbal-muscle was not attached to the inner face of the tymbal, but acted, he thought, as a plectrum, eliciting sound by rubbing its tip across the ridges of the latter.

The fourth schism from the now orthodox interpretation of Réaumur was initiated by Landois (1867, 1872, 1874). Turning from his investigations on the buzzing of bees and flies, he attempted a similar explanation for cicadas— described complicated "Stimmbänder," bordering the third spiracles, which he named "Schrillstigmen" and announced as the sole instrument of sound. The tymbal-muscles he waved airily aside—

> "Die Trommelmuskel ist stark chitinisirt und wurde von älteren Forschern einfach als Chitinstäbchen gedeutet. Die Muskelstructur desselben kann nach der microscopischen Untersuchung durchaus nicht zweifelhaft sein. Wegen seiner starken Chitinisirung kann dieses Täbchen nicht contrahirt werden." (1872, p. 348.)

He calls Aristotle to the support of his theory, and concludes triumphantly—

> "So kommt man oft durch genaue mikroscopische Studien wieder auf das zurück, was die Völker vor Jahrtausenden richtig geahnt und benannt haben." (1867, p. 158.)

Landois's view, severely and effectively criticised by his countryman Graber (1872), by Lloyd Morgan, and by Haswell, to mention only a few, was nevertheless accepted by Darwin (1871, p. 350), by Huxley (1878, p. 377), and by a large number of text-books.

c. ACCESSORY STRIDULATING APPARATUS OF TETTIGADINÆ.

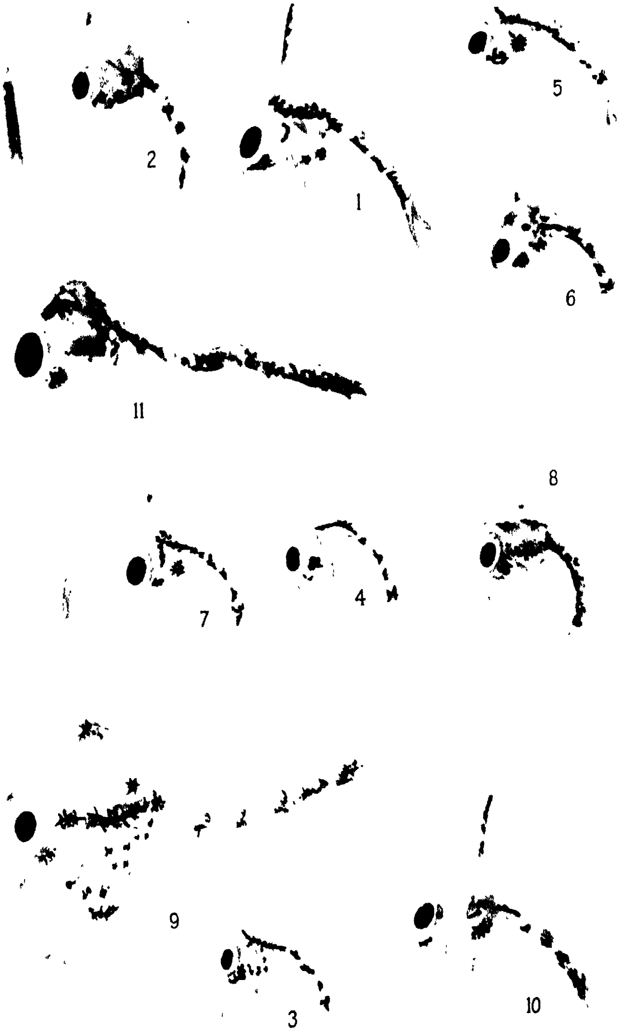
Jacobi (1907 *c*) was the first to signalise in the family Cicadidæ the existence of a second sound-producing apparatus of a far less anomalous and complicated character than the one we have just studied.

The subfamily Tettigadinæ, poor in genera and species, is essentially a neotropical group of fairly large, robust forms, with extremely well-developed tymbals, richly ribbed. On the lateral angle of the mesonotum is an inconspicuous oval area without hair, but with a series of striæ running parallel to the long axis of the body, and thus across the oval area, to which they are confined. In *Tettigades chilensis* A. & S., according to Jacobi, the ruts are not perpendicular to the surface, but inclined to form short scales. We have been able to examine only *Chonosia crassipennis* (Walk.), in which we have counted some 30 of these ridges (text fig. 59). Jacobi states that there are between 15 and 35 in all species of *Tettigades* and *Chonosia* studied, but only about 6 in *Babras*.

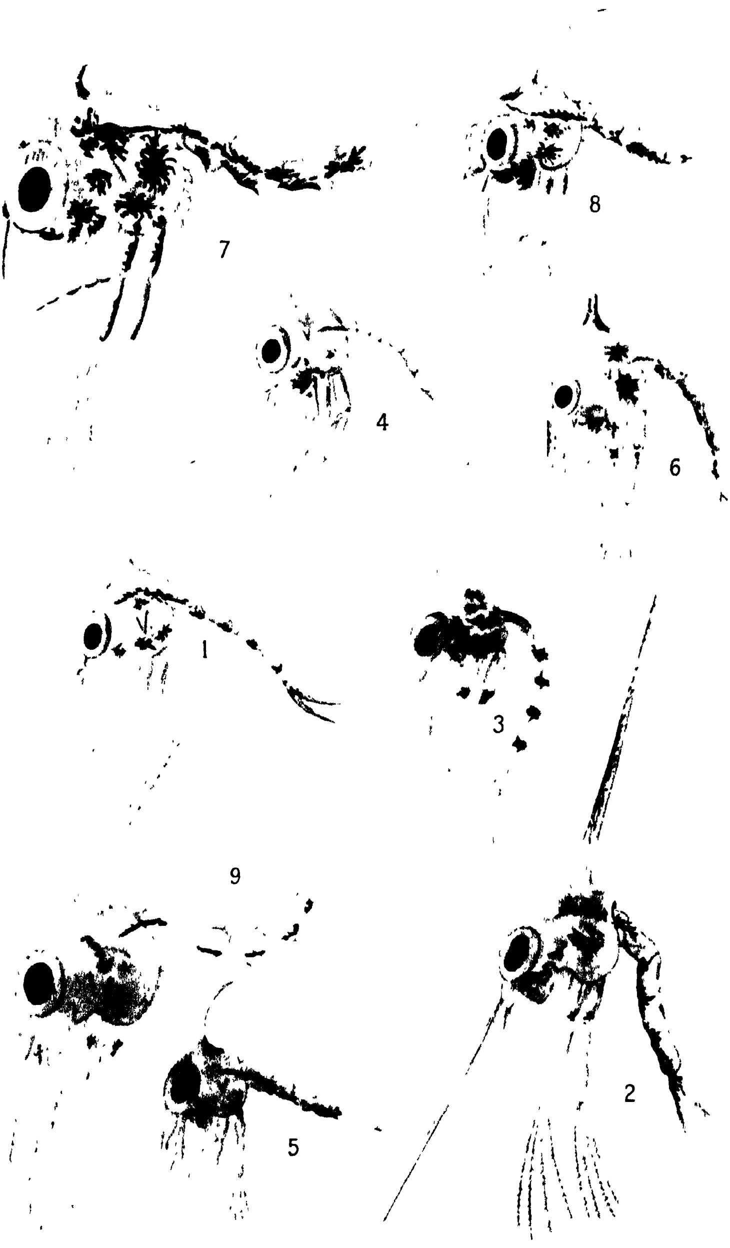
While in other cicadas the hind-base of the clavus forms approximately a right angle (*posterior tuberosity* of Amans), in *Tettigades* and *Chonosia*, according to Jacobi, it is drawn out, while in *Babras*, it is extended much further into a rounded lobe. This is the plectral portion of the stridulatory apparatus. But no one has yet recorded observations in the field to establish these assumptions, and we confess that in *Chonosia crassipennis* the anal lobe (text-fig. 59, *pt.*) seems little more developed than in ordinary cicadas, though apparently capable, nevertheless, of rubbing on the stridulatory surface (*sa.*).

This apparatus is equally developed in both sexes, and is explained by Jacobi as a "Schreckmittel" against such enemies as birds, the abdominal sound-organs being devoted to sexual purposes. We should like field-observations.

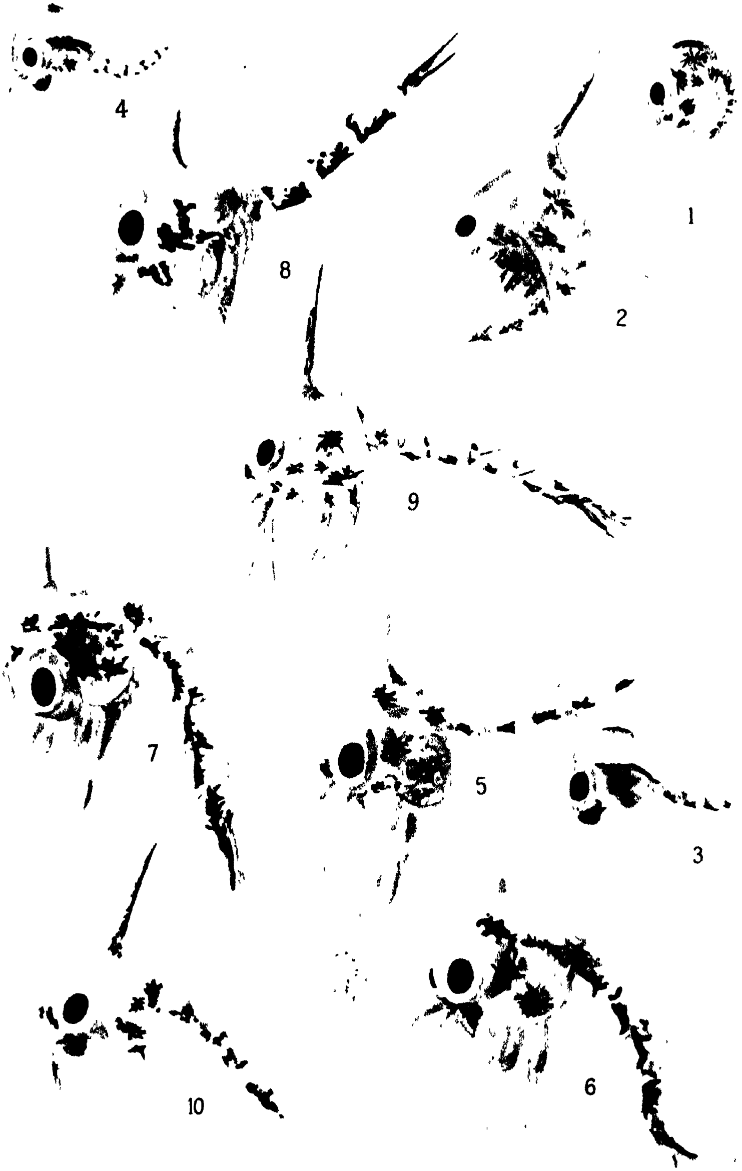
In two of our largest New Zealand cicadas, *Melampsalta cingulata* and *M. strepitans*, there is a loud wing-clicking produced by both sexes and additional to the male's song. It results from a rapid lateral movement of the wings from the roof-like resting position to one at an acute angle with the body; but the movement is so quick that it is impossible to be sure whether the noise is produced by friction between tegmina and hind-wings on each side, or between one or both pairs and the body. If the latter, then the development of the stridulating areas on the mesonotum of the Tettigadinæ is only a further step in the same direction.



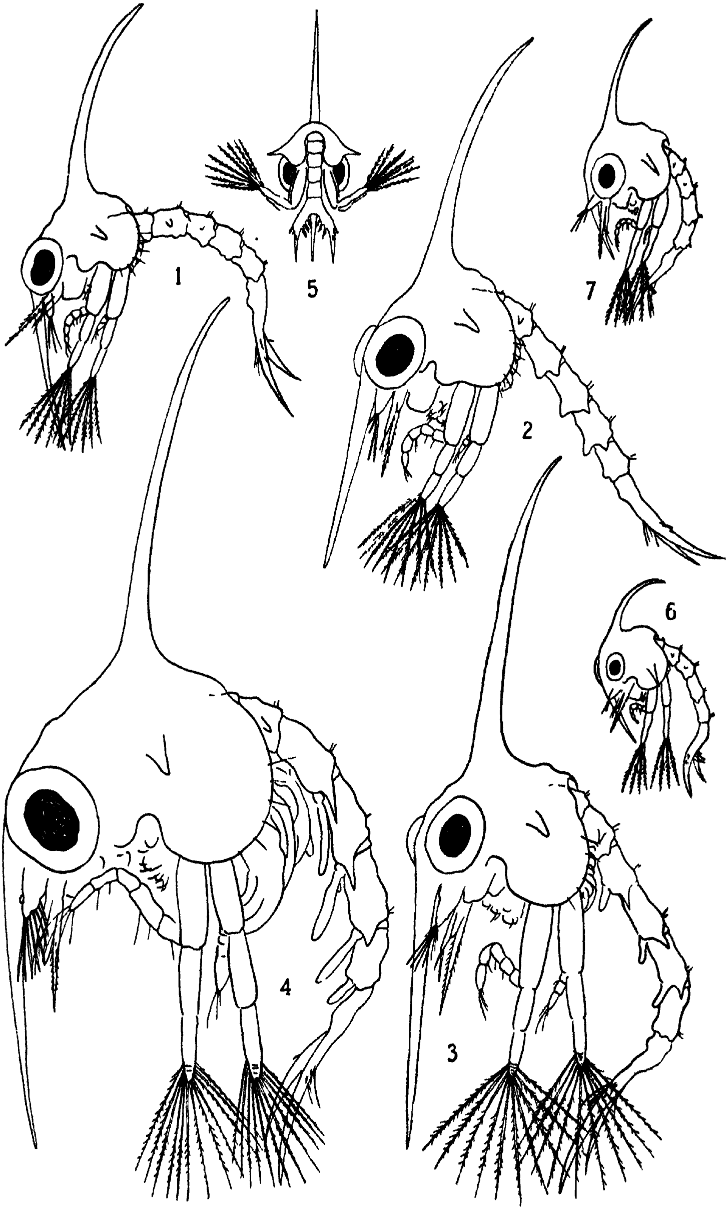
LARVAL STAGES OF THE PLYMOUTH BRACHYURA.



LARVAL STAGES OF THE PLYMOUTH BRACHYURA.

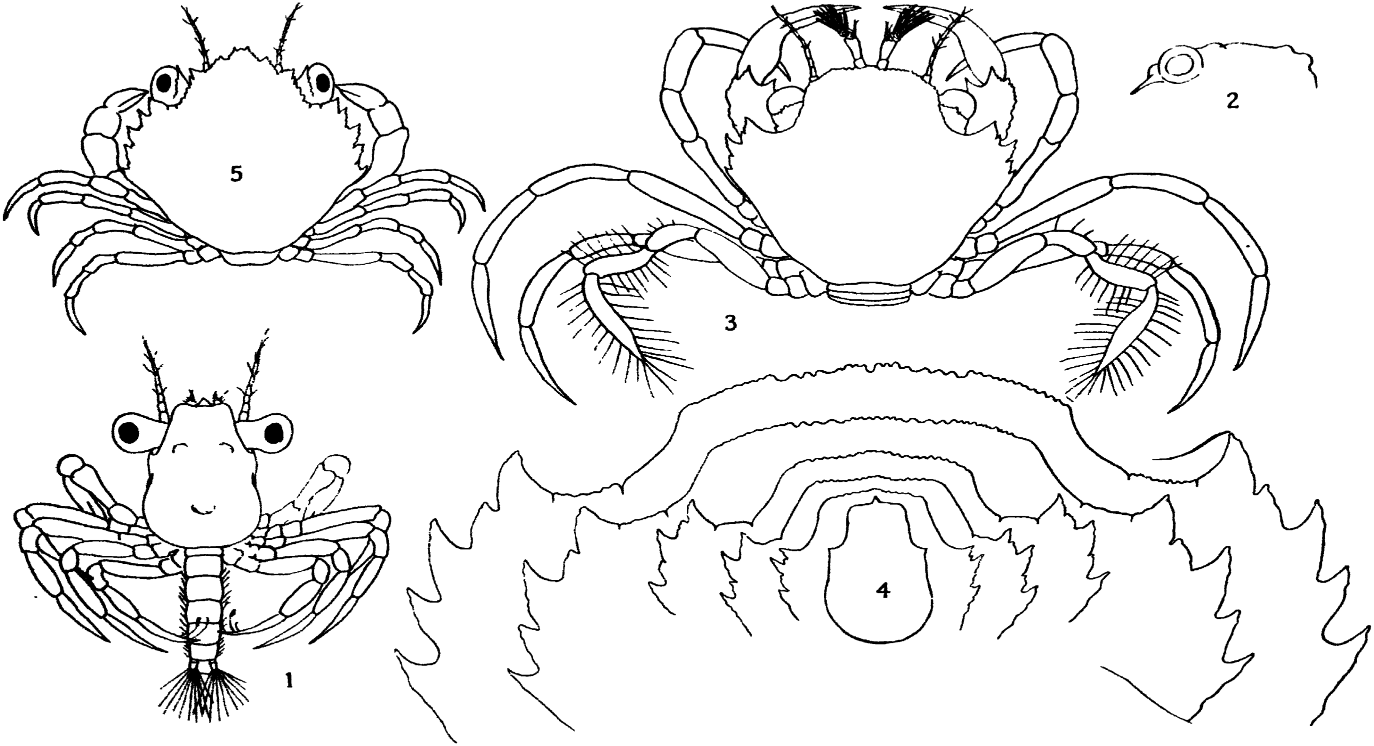


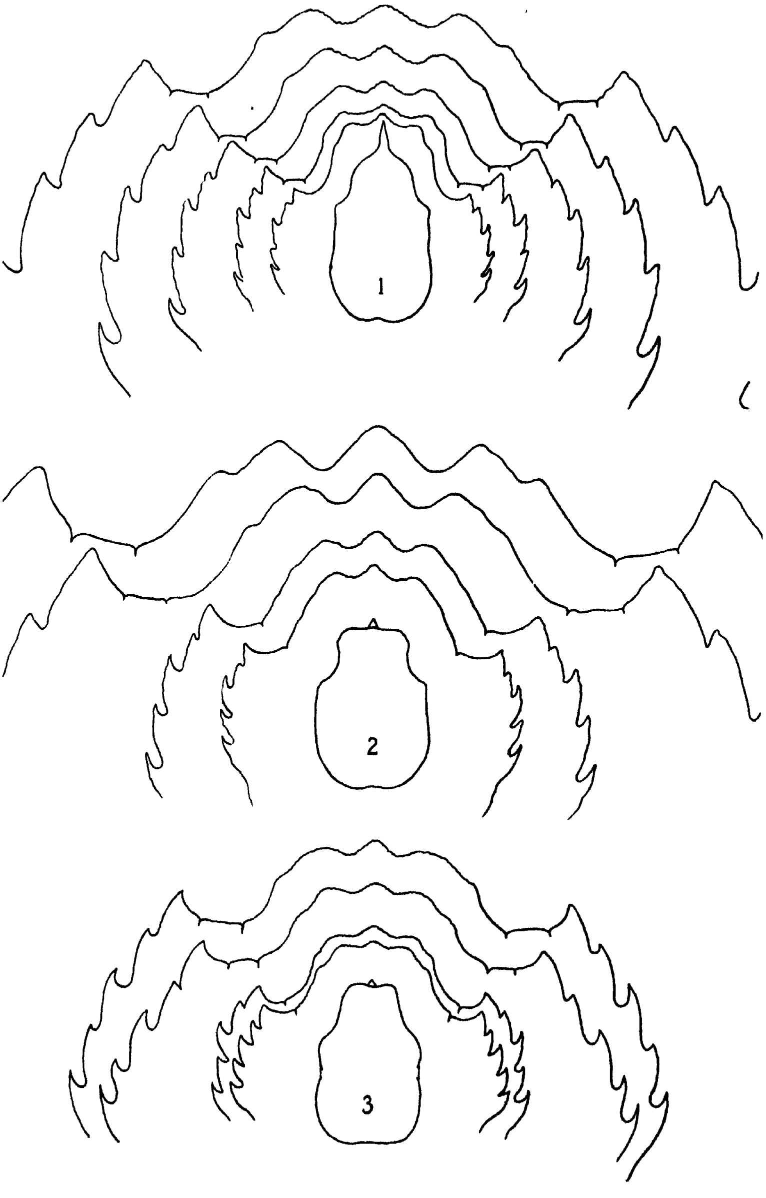
Larval Stages of the Plymouth Brachyura.



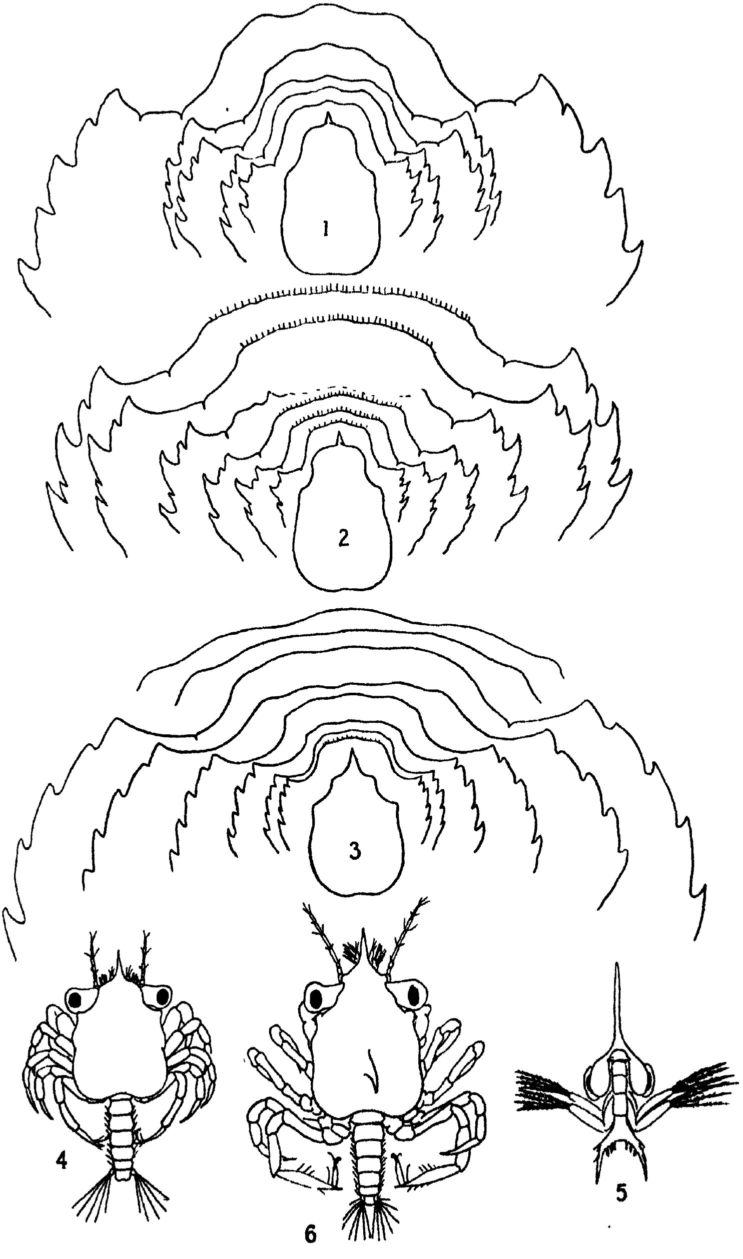
Larval Stages of the Plymouth Brachyura.

P.Z.S.1928.Lebour.Pl.V

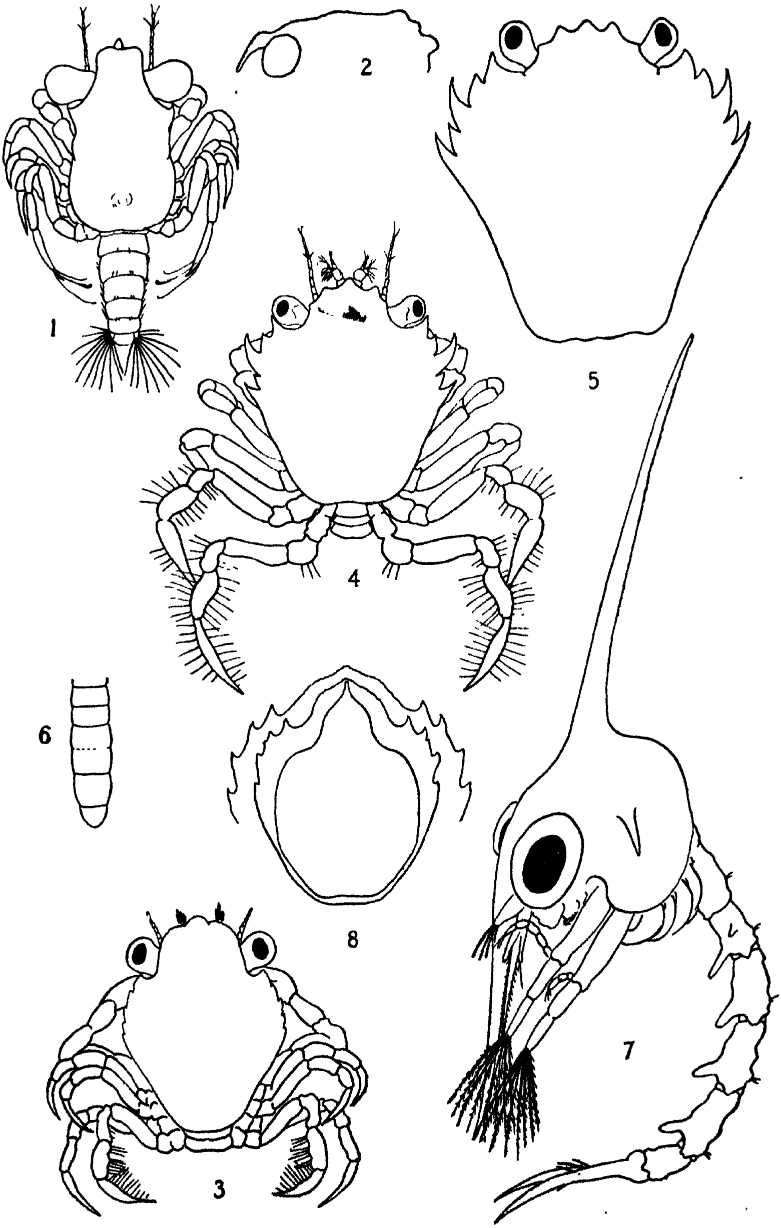




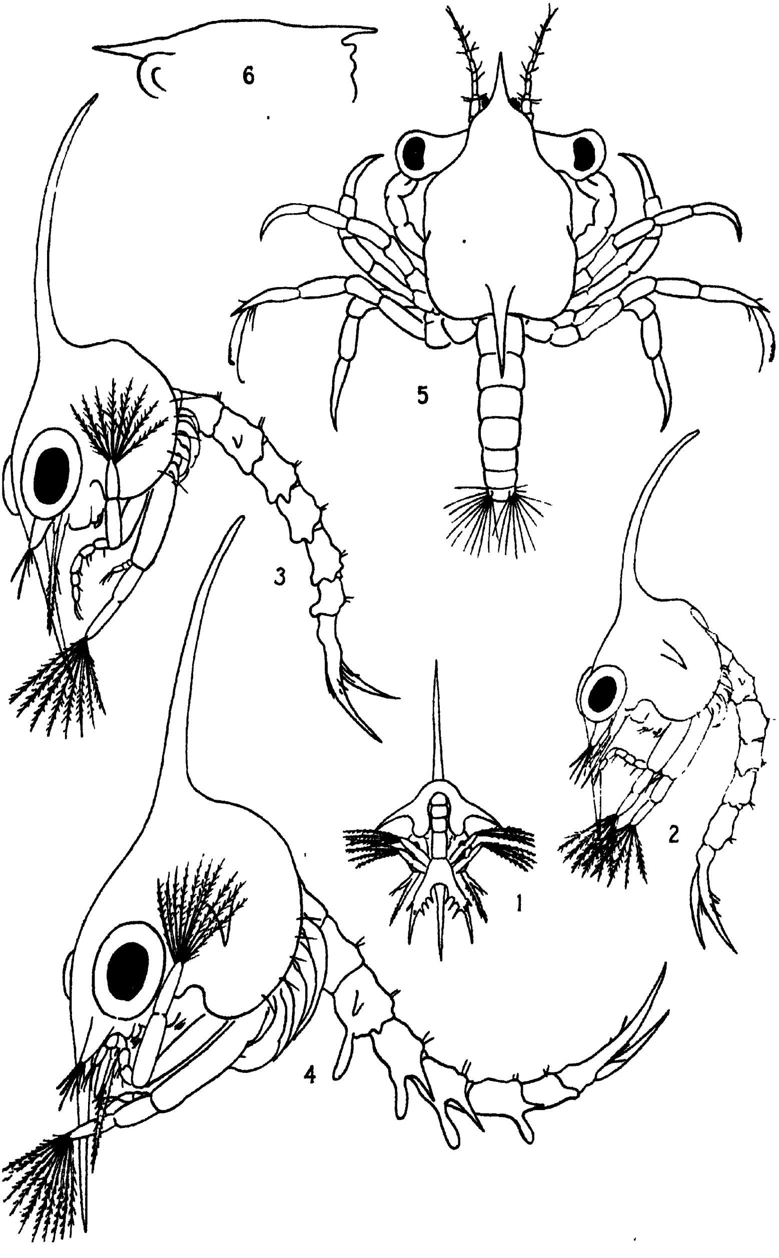
LARVAL STAGES OF THE PLYMOUTH BRACHYURA.



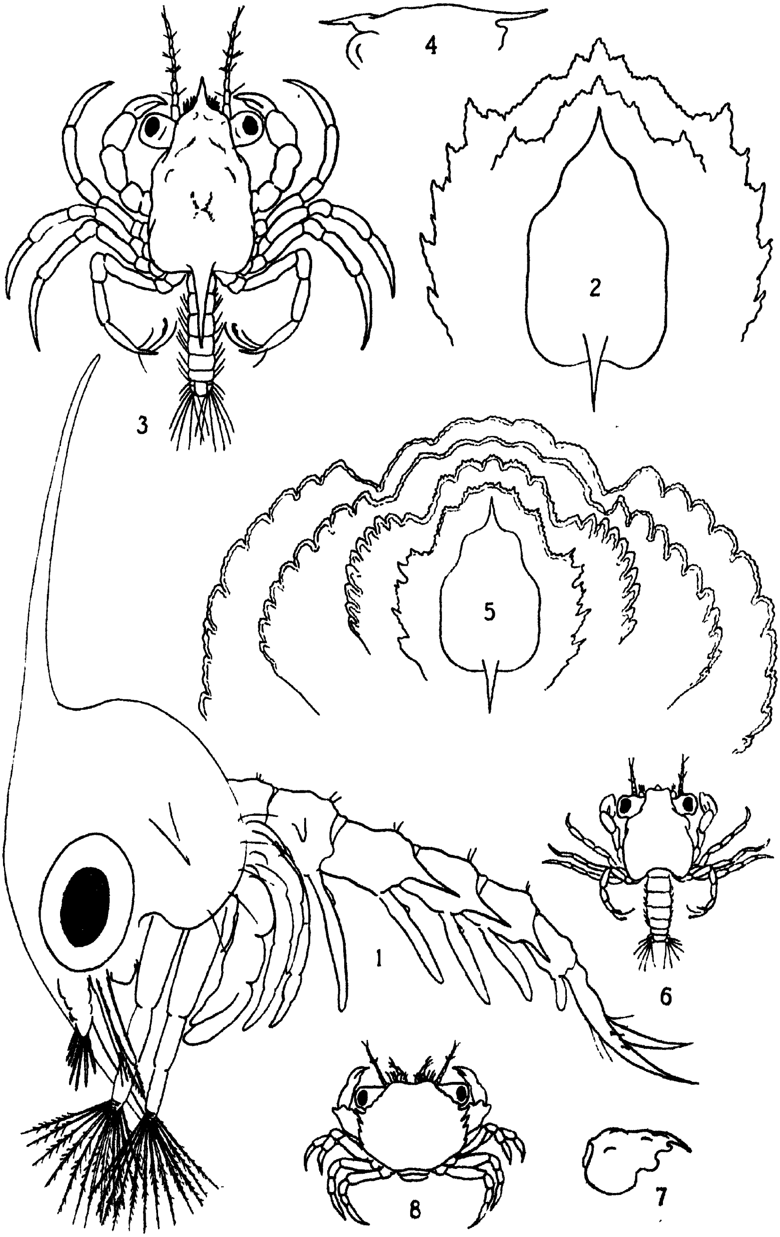
Larval Stages of the Plymouth Brachyura.



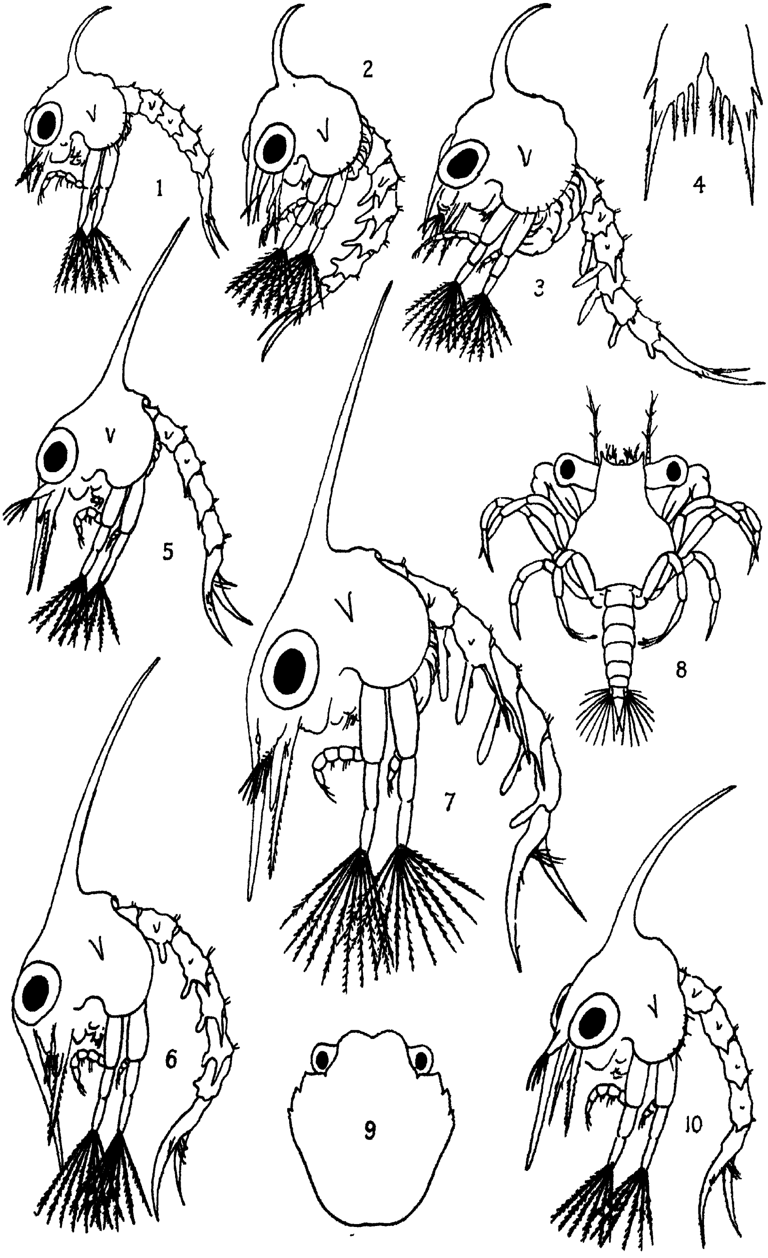
Larval Stages of the Plymouth Brachyura.



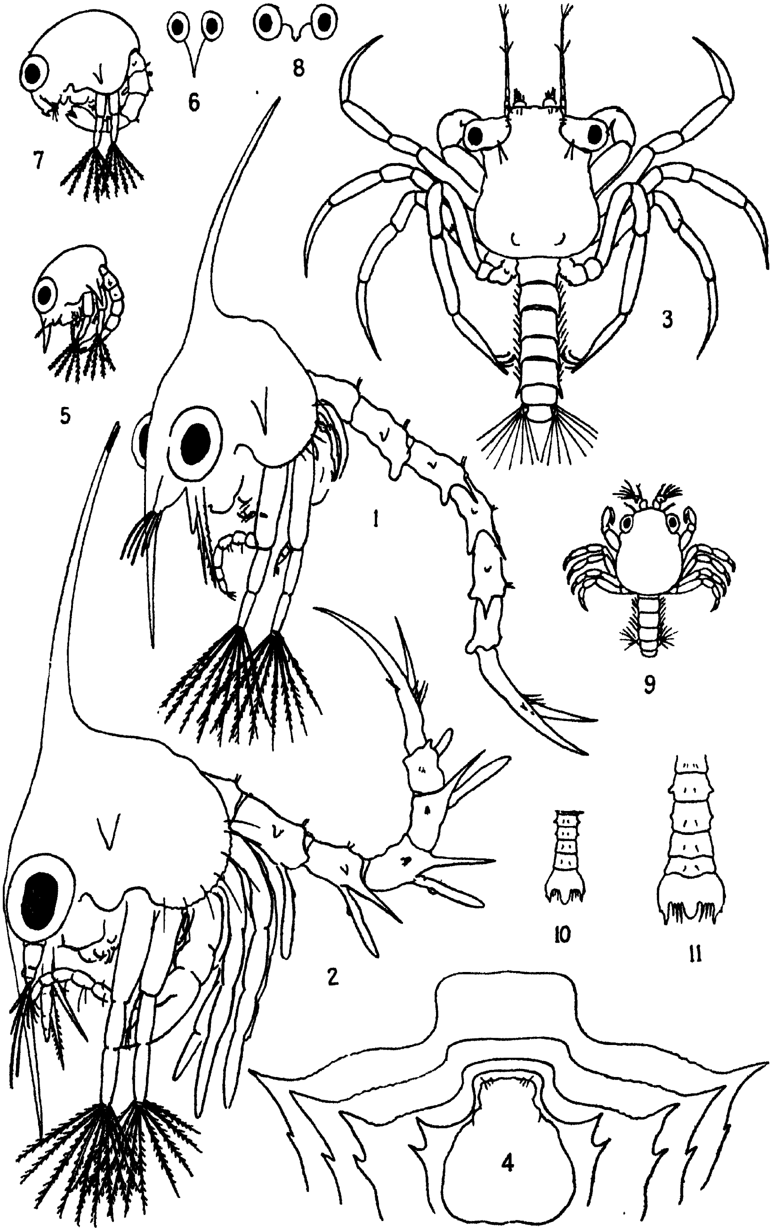
LARVAL STAGES OF THE PLYMOUTH BRACHYURA.



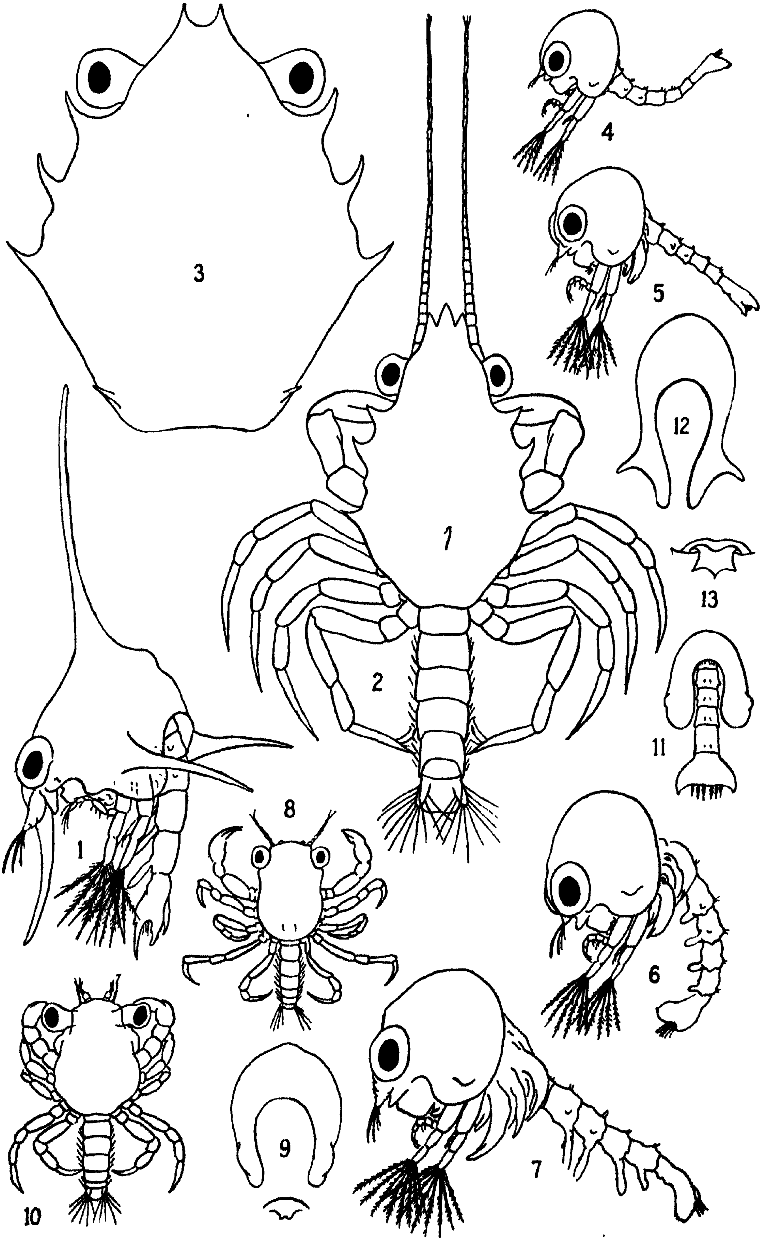
Larval Stages of the Plymouth Brachyura.



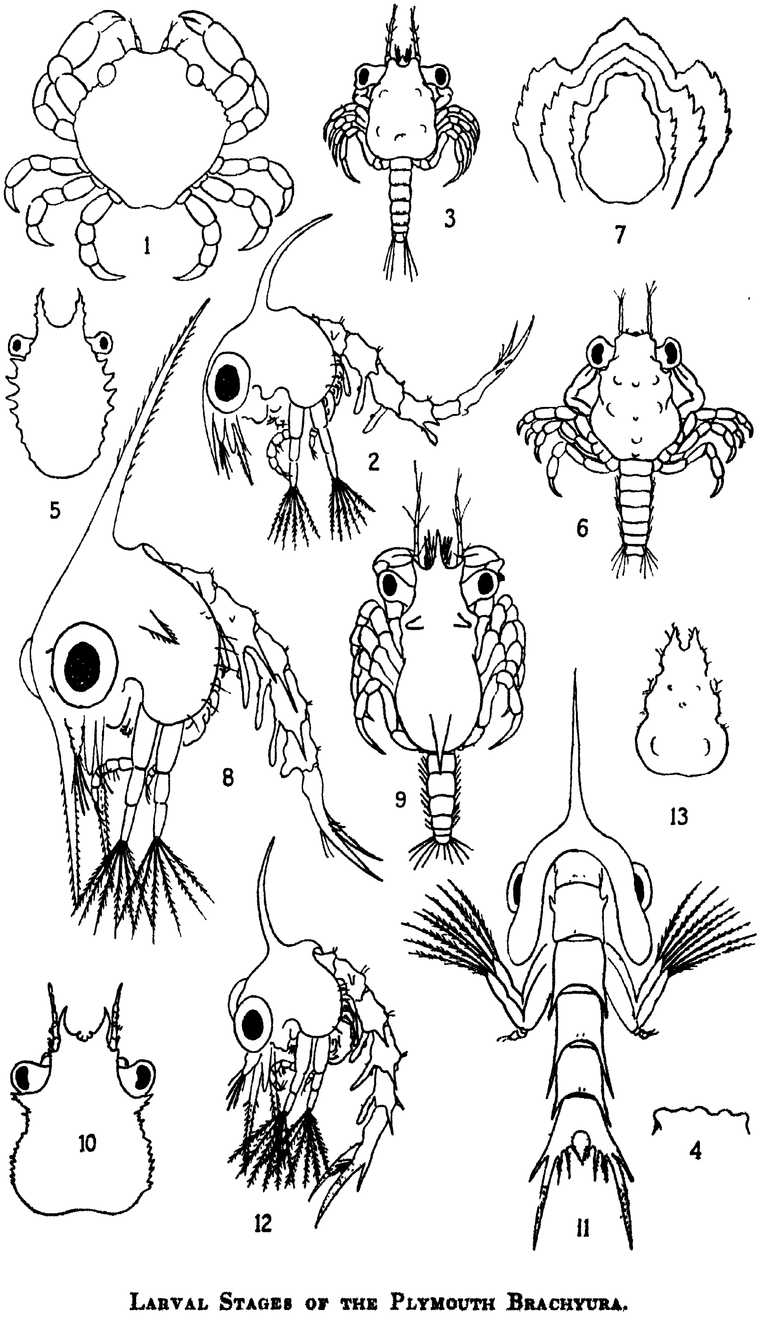
LARVAL STAGES OF THE PLYMOUTH BRACHYURA.



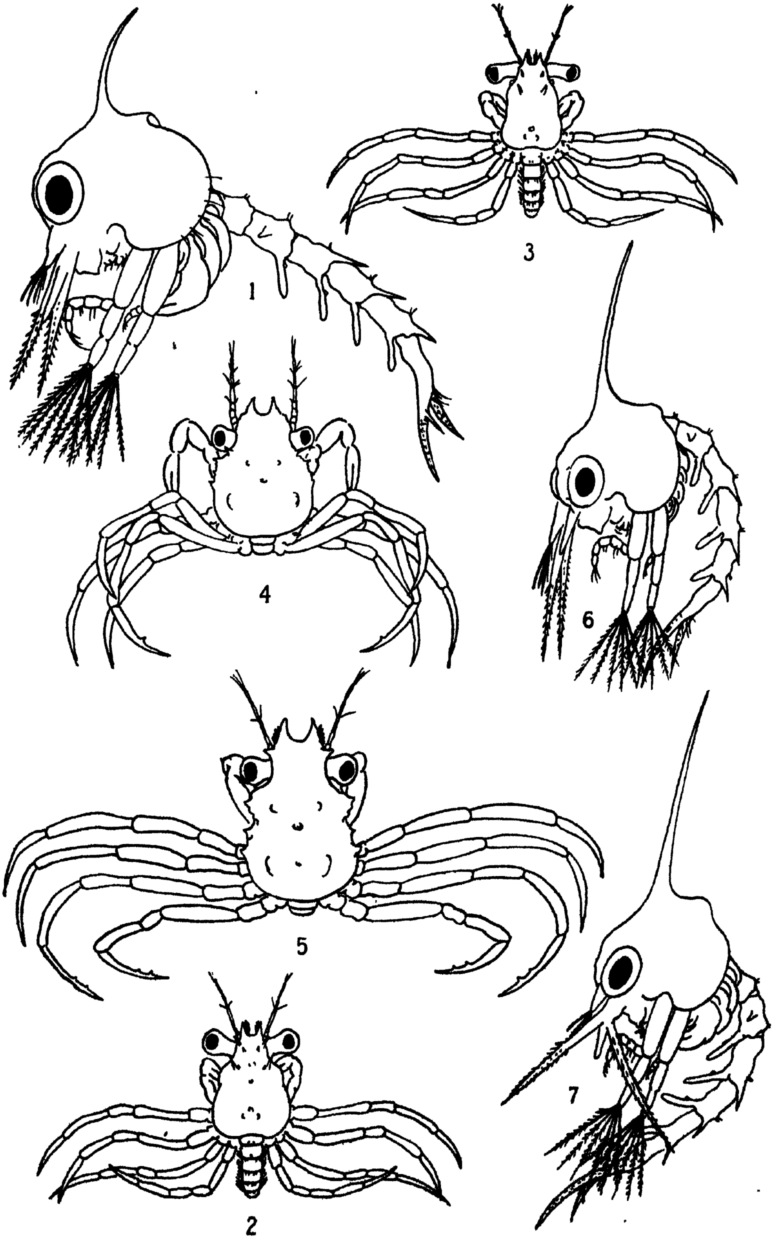
Larval Stages of the Plymouth Brachyura.



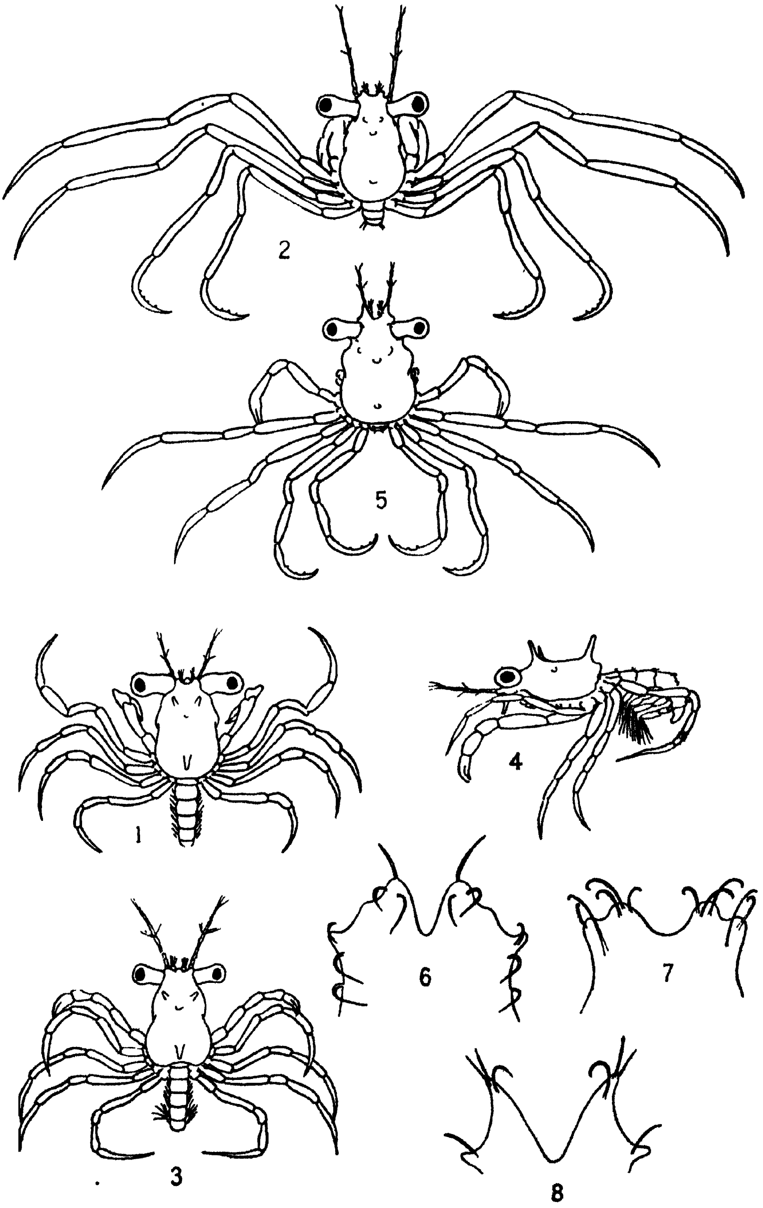
Larval Stages of the Plymouth Brachyura.



LARVAL STAGES OF THE PLYMOUTH BRACHYURA.



Larval Stages of the Plymouth Brachyura.



Larval Stages of the Plymouth Brachyura.

20. The Larval Stages of the Plymouth Brachyura.

By MARIE V. LEBOUR, D.Sc., F.Z.S., Naturalist at the Plymouth Laboratory.

[Received January 26, 1928: Read March 20, 1928.]

(Plates I.–XVI.; Text-figures 1–5[*].)

The present work is a survey of all the larval crabs which have been studied in the neighbourhood of Plymouth. Two preliminary papers have already been published on this subject (Lebour 1927, 1928), on certain Spider-Crabs, Pea-Crabs, and *Ebalia*; the remaining species are described here so far as they are known. Further work has resulted in the rearing from egg to crab of three species, from egg to megalopa of several more, and others have been reared through some of their larval stages. It has been found necessary, however, to resort to the plankton to fill the gaps, and for the whole life-history of several species when the berried crab was not forthcoming. In nearly all cases when rearing was successful, specimens from the plankton have been kept for comparison until they changed their skins, and the life-history as observed from the reared specimens was found to be normal.

In the Plymouth district there are 37 species of Brachyura, and of these something is known, if not all, of the life-history of 33. Only four have not been identified in the larval stages here—*Ebalia tumefacta*, *Achæus cranchii*, *Pisa biaculeata*, and *Hyas araneus*, and the last two of these have been described by other workers.

Wherever possible the crab has been hatched from the egg and a coloured drawing made of the first zoea. When the first zoea was not available a later stage was substituted. In this way 30 zoeæ have been drawn in colour, 23 of which came from the pre-zoea hatched from the egg. Larvæ of the rarer crabs, which are hardly ever or seldom found in the adult state, occur at certain times of the year in plankton. In this way *Thia polita*, *Pirimela denticulata* (?), and *Pinnotheres veterum* were obtained as zoeæ and reared to the megalopæ or crabs. Others which are fairly abundant have not been found in berry, but the larvæ occur in the plankton and are recognizable. Such a crab is *Gonoplax rhomboides*, which has not been found in berry whilst these researches were being made, but whose larvæ are fairly common in late summer or early autumn[†].

---

[*] For explanation of the Plates, see p. 557.

[†] Since this paper was read, a *Gonoplax* in berry was obtained outside the Sound, April 1928. The eggs were a clear pinkish crimson, in an early stage of development, and measured 0·35 mm., later 0·4 mm. These have not yet hatched.

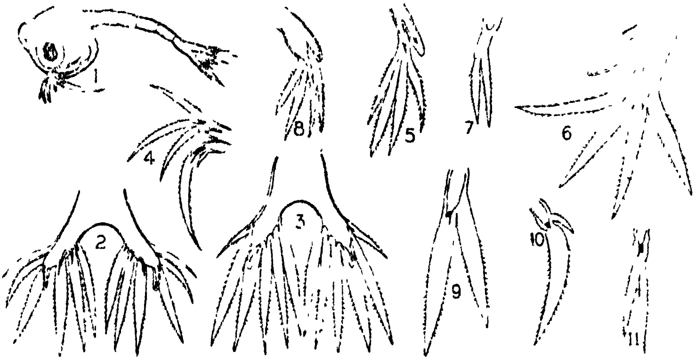
From these studies it has been found possible to distinguish the larvæ of nearly all the different genera and many of the species. Only in the few cases of very closely related genera, such as *Portunus*, *Bathynectes*, and *Polybius*, the larvæ are so much alike that, except for colour, it is almost impossible to recognize them. In a genus containing several closely-related species, such as *Portunus*, it is also sometimes difficult to distinguish some of the species. On the whole, however, most of the crab larvæ both in the zoea and megalopa can be identified.

The eggs carried by the female hatch out as pre-zoeæ, which, after a period of free existence from a few minutes only to several hours, gives rise to the first zoea. The pre-zoea is the first zoea enclosed in an embryonic skin of extreme thinness, furnished with long spines on the antennules, antennæ, and telson, and having the first two pairs of maxillipedes free from the body and biramous, but without setæ, the abdomen being unjointed. Du Cane (1839) was the first to point out the true nature of the pre-zoea, his contemporaries regarding it merely as a weak zoea not properly developed. The pre-zoea is of great interest, as it possibly has affinities with the nauplius of a penæid and may perhaps be regarded as a metanauplius (Gurney, 1926). In this work, however, it is merely regarded as an embryonic stage preceding the first larva. The larval stages with two pairs of swimming maxillipedes are called *zoeæ*, the succeeding stage, still free-swimming but with all the legs functional and swimming by means of its abdominal limbs, being called the *megalopa*.

The Pre-zoea. (Text-fig. 1.)

All the British crabs seen hatch from the egg as a pre-zoea. This is almost certainly general, except in a few cases of certain land-crabs in which the young hatch from the egg in a very advanced state. Differences in the long embryonic spines are shown in various groups, but the telson always has seven spines each side. Following Faxon (1880), these are numbered here from the inside 1 to 7. The fourth is short and not hairy, and covers the spine which in the zoea forms the tip of the fork. The seventh spine may or may not be hairy. The two spines covering the antennules may be of nearly the same length or of different lengths; those covering the antennæ may be two, three, or four, all hairy, which come from the region of the exopodite, and a non-hairy sheath covering the spinous process. Another such sheath covers the flagellum in those forms which have an abbreviated life-history, and, consequently, have the flagellum (endopodite) precociously developed. Faxon (*op. cit.*) describes and figures the pre-zoea of *Carcinus* very accurately. In the Brachyrhyncha the telson has the seventh spine usually non-hairy, although occasionally it may have a few hairs. It is often shorter than the others. The antennule has one long and one short spine, the antenna three or four long spines over the exopodite and a simple sheath over the spinous process. As the first zoea in the Brachyrhyncha has no flagellum, there is no trace of it in the pre-zoea. There are three spines in the Portunidæ, as seen in all the species of *Portunus*, in *Bathynectes*, and in *Carcinus*, four in both species of *Xantho*, in *Pilumnus*, *Cancer*, and *Atelecyclus*. Thus, even in the pre-zoea, a natural division is seen between the Portunidæ on the one hand and the Cancridæ and Xanthidæ on the other. The Oxyrhyncha have a longer seventh spine on the telson, usually hairy; the antennule has two long spines, except in *Hyas*, in which one is appreciably shorter than the other; the

Text-figure 1.



1. Pre-zoea of *Portunus puber*.
2. Telson of same.
3. Telson of pre-zoea of *Macropodia rostratus*.
4. Antennule and antenna of pre-zoea of *Portunus puber*
5. Antenna of pre-zoea of *Atelecyclus*.
6. „ „ *Macropodia*.
7. „ „ *Ebalia tuberosa*.
8. „ „ *Pilumnus*.
9. Antennule „ *Macropodia*.
10. „ „ *Atelecyclus*.
11. „ „ *Ebalia*.

antenna has four setæ over the exopodite, a simple sheath over the spinous process, and, in addition, there is a simple sheath over the flagellum which is present in the first zoea, except in *Hyas*, where it is so rudimentary that no sheath is visible. In *Ebalia*, belonging to the Leucosiidæ in the Oxystomata, the seventh spine of the telson is long and somewhat hairy, the antennule has two long spines, and the antenna, merely a rudimentary stump in the zoea, has two long spines. *Ebalia* resembles the Oxyrhyncha more than the Brachyrhyncha, the antenna differing from both.

There are thus seen to be three types of pre-zoea agreeing with the three main groups into which the Brachyura is usually divided. It is almost certain, however, that the Leucosiidæ are not typical of the Oxystomata, as they are peculiarly modified; and we know that some of the genera placed in this group are quite different from *Ebalia*, having well-developed antennæ and being modified in a quite different direction (*Ethusa*, *Dorippe*). Cano (1893) shows three spines covering the exopodite in *Dorippe* and one on the antennule, the seventh spine of the telson being hairy.

The Zoeal Stages.

From the pre-zoea emerges the first larval stage, or first zoea. The zoea is flattened from side to side, is provided with antennules, antennæ, compound eyes, mandibles, first and second maxillæ, first and second maxillipedes which are used as swimming-organs, and rudimentary third maxillipedes and walking-legs, all more or less well developed and wholly or partly hidden by the carapace. The carapace may be armed with spines, dorsal, rostral, and lateral, any or all of which may be absent, but typically the dorsal and rostral spines are long, the laterals short. The edge of the carapace is smooth or denticulated in the first zoea, or may have long hairs which are usually present in the later stages. The abdomen is not covered by the carapace, and consists typically of five joints plus the telson in the early stages and six plus the telson in the later stages. The telson is typically forked and bears spines.

The telson is adapted for keeping up in the surface-layers, the outgrowths of the carapace and abdomen being adaptations for this end, the long spines being mainly for directive purposes. In rare cases the outgrowths have almost disappeared (Leucosiidæ and some Pinnotheridæ), and in these forms the zoea usually lives near the bottom.

There may be two, four, or five zoeal stages. So far as is known, a crab with three zoeal stages has not been seen.

The *antennules* in all but the last zoea are simple, unjointed, and armed with æsthetes and spines. In the last zoea, however, they are usually jointed and biramous.

The *antennæ* typically consist of a basipodite with long spinous process and an exopodite, the endopodite (flagellum) usually arising later. In those crabs, however, with only two zoeæ the flagellum is present, if only in a rudimentary state, in the first stage. The *mandibles* (text-fig. 4, 20, 24) are bilobed, very heavy, and usually bear a simple palp in the last stage. The first *maxillæ* (text-fig. 4, 21, 22, 26), or maxillules, vary little. There is a short and narrow exopodite, one- or two-jointed, bearing several setæ, and two large endites which may be slightly subdivided, both bearing several setæ. The *second maxilla* (text-fig. 4, 23, 25, 27), or maxilla, bears a large plate-like exopodite (the scaphognathite) with few setæ in the first zoea, in the last zoea surrounded by many, and three inner lobes with five or six endites, all bearing several setæ.

The *first* and *second maxillipedes* are modified in the zoea as swimming-organs. Each consists of a strong base with an exopodite of one or two joints bearing long setæ, and an endopodite of five joints in the first maxillipede, of three, or rarely two only, in the second maxillipede. The first zoea always has four swimming-setæ on the maxillipedes, the second six, and, in those crabs which have more zoeal stages, the third usually has eight, the fourth ten, and the fifth twelve. The only exceptions in the British species, so far as is known, are *Ebalia*, which has four zoeal stages, the second and third both having six setæ, the fourth eight, and *Corystes*, which has ten in the third zoea, twelve in the fourth, and fourteen in the fifth. There are, however, cases known in some foreign crabs where there are ten setæ in both fourth and fifth stages (Hyman, 1920, in a species of *Gelasimus*), and there may at times be nine instead of ten setæ, or the normal numbers may vary slightly now and then in this way; but this seems to be unusual, and, generally speaking, the above statements appear to hold good.

The remaining limbs are rudimentary in all the zoeal stages, although traces of them are usually present under the carapace in the youngest zoeæ. In the last, or even in the penultimate zoea, the third maxillipede is usually bilobed, the first leg chelate and more or less jointed, and the remaining legs more or less jointed. None of these, however, function as walking-legs in any of the zoeal stages. The gills corresponding to the various limbs gradually appear.

The *abdomen* consists of five segments plus the telson in the early stages and six plus the telson in the later stages, except in those forms which normally have the last segment fused with the telson, in which case there are five segments plus the telson in all the zoeæ. There are no pleopods on the first abdominal segment in any of the larvæ, but they are present as rudiments on the second to the fifth segments from the first, second, or third stage onwards, becoming long and biramous, but still without setæ in the last stage. The fifth pair of pleopods on the sixth abdominal segment is often smaller than the others, and is rudimentary or absent even in the last stage, when the sixth segment is fused with the telson. The last zoeal stage can be recognized by the length of the pleopods.

The abdomen always bears a pair of more or less hook-like lateral knobs on the second segment in all zoeal stages. Further pairs of knobs, usually less hook-like, may occur on the third or, very rarely, on the fourth and fifth segments. In those species having them on the second and third segments only, those on the third may disappear in the later stages. The abdominal segments also bear fine hairs dorsally, and may have lateral outgrowths in the form of spines at the hindmost corners. These spines usually only occur in the later stages, and generally only on the second to the fifth segment, although they may be present earlier and on other segments.

The *telson* is typically forked, and always bears six setæ inside the fork. In the British Pinnotheridæ it tends to be plate-like, having three lobes with three setæ each side between the central and lateral lobes, and outside lateral denticulations may or may not be present. In *Ebalia* the telson is also plate-like, slightly emarginate behind with the six setæ in the centre, and outside lateral denticulations may be present or absent. In all the other British crabs the telson is forked, and may have three, two, or one outside lateral spine (even none at all in some foreign species). When there are three, in the later stages one or two may disappear. In the centre of the fork in the later stages one, two, three or four pairs of extra internal setæ may occur.

The characters used in the identification of the zoeal stages are the following:—

Number of zoeal stages.
Presence or absence of spines on the carapace.
Character of antennæ.
Character of telson and its armature.
Armature of abdominal segments.

The Number of Zoeal Stages. (Text-fig. 2.)

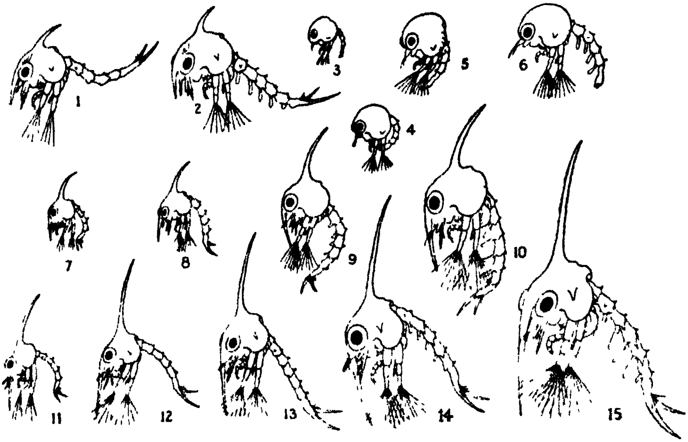
The number of zoeal stages may be five, four, or two. None are at present known with three. Certain foreign land-crabs forgo the larval stages altogether and hatch out in a state resembling the adult (Potamonidæ).

In the whole of the Oxyrhyncha so far known there are only two zoeal stages (text-fig. 2, 1, 2), with the possible exception of some of the Parthenopidæ, whose larval stages are described by Cano (1823 *a*) as being more like the Brachyrhyncha. It is possible, however, that these were not correctly identified.

Pinnotheres veterum has apparently only two zoeal stages, *Ebalia* four, but this genus is peculiar in having the second and third stages each with six setæ on the maxillipedes, the fourth with eight (text-fig. 2, 3, 4, 5, 6). There are four in *Carcinus* (text-fig. 2, 7, 8, 9, 10), *Xantho*, *Pilumnus*, *Pirimela* (?), *Gonoplax*, and *Thia*, with four to ten setæ on the maxillipedes in the respective stages, and five in *Portunus*, *Cancer* (text-fig. 2, 11, 12, 13, 14, 15), and *Atelecyclus* with four to twelve setæ on the maxillipedes in their respective stages. *Corystes* is exceptional in having ten setæ in the third, twelve in the fourth, and fourteen in the fifth stage. It is to be noted, however, that the American species, *Cancer amœnus* (Herbst), is found by Conolly (1923) to have only four zoeal stages, the last having 11 and 12 setæ.

The number of zoeal stages is important to a certain extent in distinguishing the various forms, as it is easy to see that if a zoea be far advanced in development but has few setæ on the maxillipedes, it must have only a few zoeal stages, and in this way certain genera may be eliminated. From the state of the pleopods, together with the number of setæ on the maxillipedes, we can usually tell approximately how many zoeal stages there are. Thus, if the pleopods are long and the setæ only six, we must have a Spider-Crab or a *Pinnotheres*; if long with eight setæ, an *Ebalia*; if long with ten setæ, almost certainly *Carcinus*, *Pilumnus*, *Xantho*, *Gonoplax*, *Thia*, or *Pirimela* (?)—all of which can be distinguished from one another by other characters; if long with twelve setæ, it is almost certainly *Portunus* (including *Bathynectes* and *Polybius*), *Cancer*, or *Atelecyclus*; if long with fourteen setæ, *Corystes*.

Text-figure 2.



1–2. *Maia squinado*, first and second zoea.
3–6. *Ebalia tuberosa*, first to fourth zoea.
7–10. *Carcinus mænas*, first to fourth zoea.
11–15. *Cancer pagurus*, first to fifth zoea.
(All drawn to scale.)

The above remarks apply to the British species.

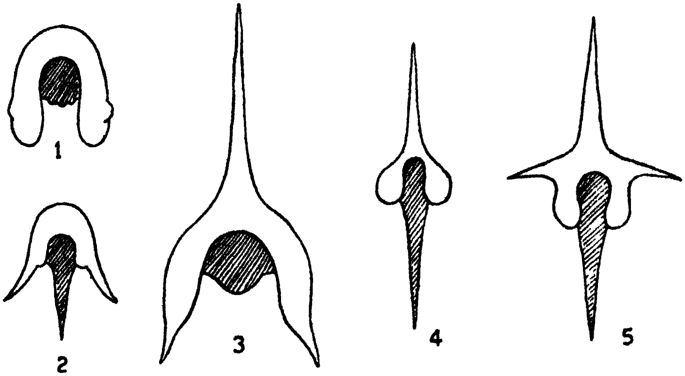
THE SPINES ON THE CARAPACE. (Text-fig. 3.)

The spines on the carapace are rudimentary, very small, or absent in *Ebalia* (text-fig. 3, 1), where there is no dorsal spine at all, a very short remnant of a rostral spine, and very short laterals which may be reduced merely to rounded prominences. The dorsal spine is also absent in *Pinnotheres pisum* (text-fig. 3, 2), which has well-developed rostral and lateral spines, the rostral probably being reduced in the later stages. In the Inachinæ there is only a dorsal spine (text-fig. 3, 3), the rostral and laterals being absent, and the lateral spines are absent in *Carcinus* (text-fig. 3, 4), *Pirimela* (?), and *Eurynome*. In all the other British species there are well-developed dorsal, rostral, and

"

lateral spines (text-fig. 3, 5). Too much importance must not be attached to these spines except for convenience in identification. They are clearly developed for use in directing movement and keeping up the surface-layers, and their reduction appears to be associated with habits near the bottom. Closely-related species may or may not have certain spines; for instance, *Portunus* has them all, *Carcinus* has no laterals, and *Pinnotheres veterum*, although possibly belonging to another genus, is closely related to *P. pisum*, and yet one has all the spines and the other has no dorsal.

Text-figure 3.



1. Carapace of *Ebalia* (from behind).
2. „ „ *Pinnotheres pisum* (from behind)
3. „ „ *Inachus* (from behind).
4. „ „ *Carcinus* „ „
5. „ „ *Portunus* „ „

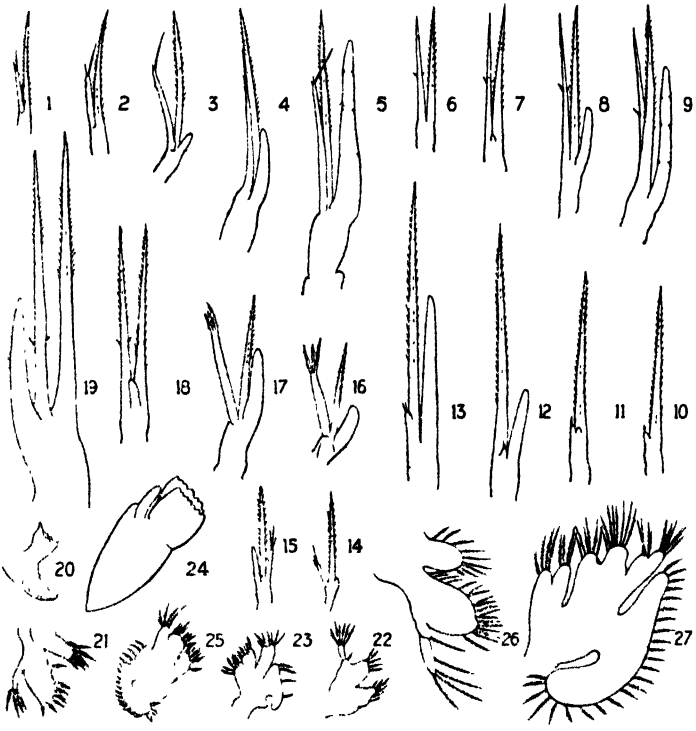
(All drawn to scale.)

THE CHARACTER OF THE ANTENNÆ. (Text-fig. 4.)

The antennæ are rudimentary stumps in *Ebalia* and *Pinnotheres*, but are well developed in all the other genera. Excluding the Pinnotheridæ in the remaining British Brachyrhyncha, and apparently in foreign species also so far as they are known, the first zoea has no flagellum (endopodite), or only a trace of one, the spinous process and the exopodite being well developed [except in *Xantho* (text-fig. 4, 10 to 13) and some of its foreign relatives, where the exopodite is rudimentary].

In the Oxyrhyncha the flagellum is present in the first (text-fig. 4, 16 to 19) zoea, even in *Hyas* (text-fig. 4, 14, 15), where it is very small, and is well grown in the second (last) zoea. The exopodite may be long or short, the spinous process always long in both Brachyrhyncha (except the Pinnotheridæ) and the Oxyrhyncha.

Text-figure 4.



1–5. Antenna of first to fifth zoea of *Atelecyclus*.
6–9. „ „ first to fourth zoea of *Gonoplax*.
10–13. „ „ „ „ *Xantho*.
14–15. „ „ first and second zoea of *Hyas*.
16–17. „ „ „ „ *Maia*.
18–19. „ „ „ „ *Inachus*.
20. Mandible of first zoea of *Inachus*.
21. First maxilla of second zoea of *Inachus*.
22. First maxilla of first zoea of *Cancer*.
23. Second maxilla of first zoea of *Cancer*.
24. Mandible of fifth zoea of *Atelecyclus*.
25. Second maxilla of second zoea of *Inachus*.
26. First maxilla of fifth zoea of *Atelecyclus*.
27. Second maxilla of fifth zoea of *Atelecyclus*.

(All drawn to scale.)

The flagellum in the Brachyrhyncha (text-fig. 4, 1 to 9) usually appears in the second or third stage, gradually growing longer in the fourth and fifth, and may or may not be slightly jointed. In *Corystes* it is very long in the later stages, much longer than the spinous process in the last zoea. The exopodite is as long or nearly as long as the spinous process in the Inachinæ, in *Pilumnus*, and in *Gonoplax* (text-fig. 4, 6 to 9), and is a good deal shorter than the spinous process in *Maia* (text-fig. 4, 16, 17), *Hyas*, *Eurynone*, and the rest of the Brachyrhyncha.

Cano (1892 *b*) regards the long exopodite as a primitive feature, as it is homologous with the antennal scale of the Caridea, but its presence in such widely-separated forms as the Inachinæ, *Pilumnus*, and *Gonoplax* makes it very important to be careful in trying to find relationships. May not the long exopodite in the Inachinæ be a compensation for the absence of the rostral spine? When in the water the two long antennal spines are usually widely spread out, and probably do help in a large way in keeping the body up. On the other hand, the rudimentary stumps in *Ebalia* and *Pinnotheres* are almost certainly acquired, and probably of use in the general reduction of outgrowth in a species living near the bottom.

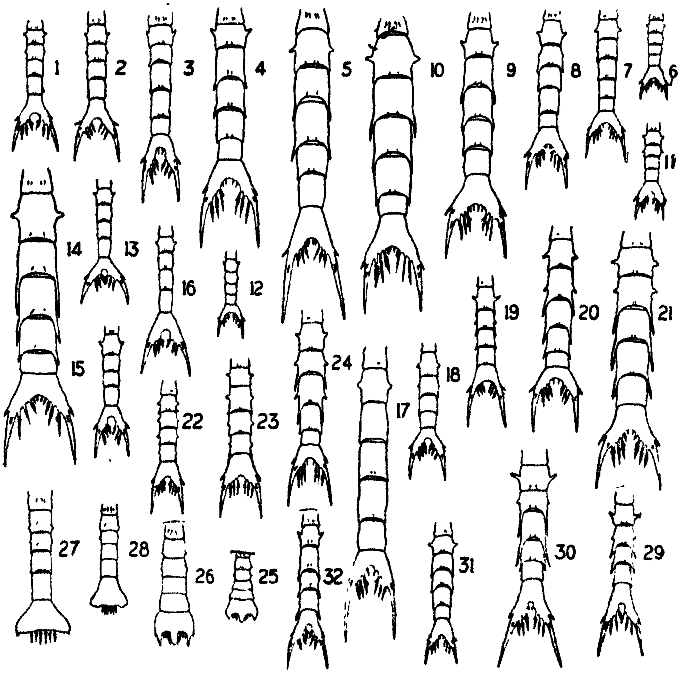
On the whole, the form of the typical antenna, with the exopodite about half, or rather more than half, the length of the spinous process, seems to belong to most of the zoeæ, which perhaps may be regarded as some of the most primitive: that is to say, the Portunidæ, the Crancridæ, and the Corystidæ; but it is also present in *Maia*, *Eurynome*, and *Hyas*.

THE ARMATURE OF THE ABDOMEN. (Text-fig. 5.)

There is a more or less hook-like knob on each side of the second abdominal segment in all crab zoeæ. There may be a smaller and usually rounder knob on the third segment, and this may or may not disappear in later zoeæ. In *Gonoplax* (text-fig. 5, 22 to 24), alone of the British forms, there are knobs on the fourth and sometimes on the fifth segments in all stages. They are present also in *Planes*, described by Hyman (1925). In all the Oxyrhyncha, except *Hyas* (text-fig. 5, 29, 30), which has a knob on the third segment also in both zoeæ, there is only the knob on the second segment. This is also the case in *Cancer* (text-fig. 5, 15), *Atelecyclus* (text-fig. 5, 13, 14), *Pirimela* (?), *Thia* (text-fig. 5, 17), and *Corystes* (text-fig. 5, 16), in the Brachyrhyncha. In *Portunus* (text-fig. 5, 1–10), *Bathynectes* (text-fig. 5, 11), *Polybius* (text-fig. 5, 12), *Carcinus*, *Pilumnus*, and *Xantho* (text-fig. 5, 18 to 21) there are knobs on the third segment also, which persist in *Pilumnus* and *Xantho*, but in *Portunus* and *Carcinus* (*Bathynectes* and *Polybius* not being known in the later stages) disappear in the later zoeæ. In *Ebalia* (text-fig. 5, 27, 28) and *Pinnotheres* (text-fig. 5, 25, 26) there are knobs on both segments in all stages.

The significance of these knobs is difficult to conjecture. It

Text-figure 5.



1–5. Abdomen of *Portunus puber*, first to fifth zoea.
6–10. „ *P. depurator*, first to fifth zoea.
11. „ first zoea of *Bathynectes*.
12. „ „ „ *Polybius*.
13–14. „ first and fifth zoea of *Atelecyclus*.
15. „ first zoea of *Cancer*.
16. „ „ „ *Corystes*.
17. „ third zoea of *Thia*.
18–21. „ first to fourth zoea of *Xantho*.
22–24. „ first to third zoea of *Gonoplax*.
25. „ second zoea of *Pinnotheres pisum*.
26. „ „ „ *P. veterum*.
27. „ fourth zoea of *Ebalia tuberosa*.
28. „ „ „ *E. cranchii*.
29–30. „ first and second zoea of *Hyas*.
31. „ second zoea of *Eurynome*.
32. „ „ „ *Macropodia*.
(All drawn to scale.)

is possibly a primitive feature to have them on many segments, as they are present in some of the larval *Dromia* and *Homola*. In support of this is the fact that they tend to disappear in the later stages of *Portunus* and its allies. However, *Gonoplax* is the only British species to have them on more than two segments, and, apart from the long spinous exopodite, its other characters do not seem to justify its being regarded as a primitive form.

In most zoeæ there are long lateral spines in the later stages on the second or third to the fifth abdominal segments, occasionally on all, and these occur rarely, even in the earlier stages. There are no lateral spines, or only in a rudimentary state, in *Carcinus*, *Thia*, *Pirimela* (?), *Ebalia*, and *Pinnotheres*. These spines probably help to keep the zoea in the upper layers, and may be specially useful in the later stages as the body becomes heavier.

THE ARMATURE OF THE TELSON. (Text-fig. 5.)

The telson is of the typical forked form in most zoeæ. In both the British species of *Pinnotheres* (text-fig. 5, 25, 26), but not in all the foreign forms, the telson is three-lobed, with three setæ each side of the median lobe between this and the lateral lobes, and outside there may be one or several lateral teeth. The shape of the telson distinguishes *Pinnotheres* from all the other genera. *Ebalia*, also, has a very characteristic telson in the form of a flat triangular plate, somewhat emarginate behind, with six setæ in the centre, having one or several lateral teeth outside (text-fig. 5, 27, 28). The hindmost tooth, which may be the only one, corresponds with the point of the forked telson of the typical zoeæ. The telson of both *Pinnotheres* and *Ebalia* is probably an adaptation to living near the bottom, the plate curling under the body, so that the zoeæ may easily assume a ball-like shape. All the other British genera have the typical forked telson, and also all foreign forms known except the Leucosiidæ and other Oxystomata. The telson may be armed in various ways, but always has the six setæ inside the fork. One, two, three, or four pairs of extra shorter setæ may occur in the later stages inside, thus dividing the six into two groups. Outside the fork there may be three spines, which may be reduced in the later stages to two or one, or there may be two in all stages or only one. In some foreign crabs there may be no lateral spines. The number is apparently constant for the genera, except in abnormal cases. The forked telson, armed with six setæ inside the fork and three outer lateral spines each side, seems to correspond best with the armature of the embryonic cuticle and with many penæid larvæ. This form of armature is present in *Maia* and *Eurynome*, in the Oxyrhyncha and in all the Portunidæ known, also in *Xantho* and

Pilumnus. In *Maia* there are no extra internal setæ; in *Eurynome* (text-fig. 5, 31) there is an extra pair in the second zoea; in *Portunus* there is an extra pair in the second, third, or fourth, and two extra pairs in the fourth or fifth zoea. In *Portunus puber* (text-fig. 5, 1–5), alone of the genus, one outer lateral spine disappears in the later stages. In all the other *Portunus* species the three remain in all stages (text-fig. 5, 6–10). In *Carcinus* two disappear, and there are no extra internal setæ. In *Xantho* (text-fig. 5, 18–21) there are one and two extra pairs of internal setæ, whilst in *Pilumnus* there are none, and in both *Xantho* and *Pilumnus* the three lateral spines are retained in all stages. In *Xantho*, however, one lateral is so minute that it is hardly visible. In all the remaining species there are fewer lateral spines. *Cancer* (text-fig. 5, 15) and *Atelecyclus* (text-fig. 5, 13, 14) have two in all stages, the extra internal setæ appearing in the later stages as in *Portunus*. Thus the telson of the later zoeæ corresponds exactly with that of *Portunus puber*. *Gonoplax* (text-fig. 5, 22–24) has two lateral spines in all stages, with one and two extra internal pairs of setæ in the later zoeæ. *Thia* (text-fig. 5, 17) has one lateral in all stages and one extra internal pair of setæ in stages two to four. *Pirimela* (?) has one pair of laterals in the last stage (only one seen) and one extra internal pair of setæ, and *Corystes* has one lateral in all stages, but differs from all the others in having one, two, three, and four extra pairs of setæ in the second, third, fourth, and fifth stages respectively. *Hyas* (text-fig. 5, 29, 30) has two pairs of laterals in both zoeæ and an extra pair of internal setæ in the second, whilst the Inachinæ (text-fig. 5, 32) have one lateral only in all stages and no extra setæ. It is thus seen that almost every conceivable variation may be present, but that it is constant for the species and nearly always for the genus.

It seems from these facts that the telson most near the embryonic form, and therefore probably nearest the primitive form, is one armed each side with six spines or setæ plus the fork and three lateral spines each side, a lesser number of laterals in certain cases being acquired in later stages and also the internal extra setæ. These latter may perhaps be regarded as less primitive. If these be so regarded, then we have *Portunus* with the most primitive telson in the Brachyrhyncha, and *Maia* and *Eurynome* in the Oxyrhyncha. Now, the Oxyrhyncha all have very much abbreviated life-histories, and are probably not so primitive as the Brachyrhyncha. It remains, then, that if the Brachyrhyncha are to be regarded as having the most primitive zoea, *Portunus* is the most primitive of these, in spite of the fact that the adult is modified for swimming, *Portunus* having the following larval characters: many zoeal stages, a telson with three outside lateral spines, and three internal setæ each side, besides the point of the fork, making seven spines in all each side, two extra pairs of internal setæ arising later (in *Portunus puber* only one of the outside lateral spines disappears in later stages); knobs on the abdominal segments 2 and 3, those on the third disappearing in later stages; antenna with well-developed exopodite about half as long as the spinous process and ending in spines.

It thus seems legitimate to regard the Brachyrhyncha as more primitive than the Oxyrhyncha, and this fits in with the most recent classifications. There appear to be two quite definite series, one represented by the Brachyrhyncha, the other by the Oxyrhyncha, both probably descended from some unknown common ancestor. There are very definite and important characters separating the two groups, always excepting the Pinnotheridæ, which in their larval forms are certainly more like the Leucosiidæ than the Brachyrhyncha. The Oxystomata are somewhat perplexing, as the Leucosiidæ have larvæ which are not in the least like those of other members of the group. They are placed here between the Brachyrhyncha and the Oxyrhyncha.

The characters of the megalopæ given below agree with this division; but before describing these, a key of the Plymouth zoeæ is given which enables one to distinguish the genus in nearly every case. This key is based on all characters, and does not pretend to be a natural classification.

Key to the Zoeæ.

I. All spines on carapace rudimentary. Four zoeal stages (the second and third both with six setæ on the maxillipedes)	*Ebalia.*
II. Only dorsal spine present on carapace. Two zoeal stages.	
1. One large lateral spine on telson	*Inachus.*
2. One rather small lateral spine on telson	*Macropodia.*
III. Dorsal and rostral spine present on carapace; no laterals.	
1. Spines curved; length from tip of dorsal to tip of rostral about equal to, or shorter than, the body-length.	
a. Two zoeal stages. Antennal flagellum well developed in first zoea	*Eurynome.*
b. Four zoeal stages. Antennal flagellum quite rudimentary in first zoea	*Carcinus.*
2. Spines nearly straight; length from tip of dorsal to tip of rostral longer than the body-length. Four zoeal stages	*Pirimela* (?).
IV. No dorsal spine on carapace. Laterals and rostral present. More than two zoeal stages (exact number unknown)	*Pinnotheres pisum.*
V. All four spines present on carapace. Two, four, or five zoeal stages.	
1. Spines on carapace armed with spicules. Two zoeal stages	*Hyas.*

2. Spines on carapace smooth.

- *a.* Lateral spines long, curved downwards and backwards. Two zoeal stages .... *Pinnotheres veterum.*
- *b.* Lateral spines short, sticking out horizontally or slightly bent.
  - *α.* Dorsal and rostral spines each shorter than the length of the carapace.
    - × Hind border of abdominal segments denticulated. Exopodite of antenna nearly as long as the spinous process; pointed. Four zoeal stages....... .... *Pilumnus.*
    - ×× Hind border of abdominal segments not denticulated. Exopodite of antenna about two-thirds the length of the spinous process; ending in spines. Two zoeal stages . *Maia.*
  - *β.* Dorsal and rostral spines each longer or equal to the length of the carapace.
    - × Exopodite of antenna rudimentary. Four zoeal stages ... . *Xantho.*
    - ×× Exopodite of antenna well developed.
      - ○ Exopodite of antenna almost the same length as the spinous process; pointed knobs on 2nd to 4th or 5th abdominal segments. Four zoeal stages .... *Gonoplax.*
      - ○○ Exopodite of antenna from one-third to two-thirds length of spinous process; ending in spines. Not more than two pairs of knobs on abdominal segments.
        - ⊕ Telson with two lateral spines in all stages. Five zoeal stages.
          - ⊙ Dorsal and rostral spines long, nearly straight. Antennal exopodite about one-third the length of the spinous process . . . . *Cancer.*
          - ⊙⊙ Dorsal and rostral spines moderately long, curved, but straighter in later stages. Antennal exopodite half or two-thirds as long as the spinous process . ... *Atelecyclus.*
        - ⊕⊕ Telson with three lateral spines in all stages. Five zoeal stages . . .. *Portunus** (including *Bathynectes* and *Polybius*, which are only known in the first zoeal stage).
        - ⊕⊕⊕ Telson with one lateral spine in all stages.
          - ⊙ Rostral spine more than two-thirds the length of the dorsal spine. Five zoeal stages .... *Corystes.*
          - ⊙⊙ Rostral spine less than two-thirds the length of the dorsal spine. Four zoeal stages .... *Thia.*

---

* *Portunus puber* is exceptional in having the lateral spines reduced to two in the later stages (see under that species).

The Characters of the Zoeæ in Different Genera.

Genus.	Number of zoeal stages.	Spines on carapace.	Lateral spines on telson.	Knobs on abdomen.
Portunus	5	All present.	3 in all stages (except *P. puber*, where they are reduced to two in the later stages).	2 pairs reduced to 1 pair.
Bathynectes...	Probably 5	„	All present (only first zoea known).	2 pairs in first zoea.
Polybius	„ „	„	„	„
Cancer	5	„	2 in all stages.	1 pair in all stages.
Atelecyclus ...	„	„	2 „	„
Corystes	„	„	1 „	„
Thia	4	„	1 „	„
Pirimela (?)...	„	No laterals.	1 (only last zoea known).	1 pair (only last zoea known).
Carcinus	„	„	3 reduced to 1.	2 pairs reduced to 1 pair.
Xantho.... ...	„	All present.	3 in all stages.	2 pairs in all stages.
Pilumnus.. ..	„	„	3 „	„
Gonoplax... .	„	„	2 „	3 or 4 pairs in all stages.
Ebalia	„	All rudimentary.	1 to 3 in all stages.	2 pairs in all stages.
Pinnotheres pisum.	3 or 4?	No dorsal.	1 and a few denticulations.	„
P. veterum ...	2	All present.	1 in all stages.	„
Maia	„	„	3 „	1 pair in all stages.
Eurynome......	„	No laterals.	2 „	„
Hyas............	„	All present.	2 „	2 pairs in all stages.
Inachus	„	Only dorsal present.	1 „	1 pair in all stages.
Macropodia...	„	„	1 „	„

The Megalopa.

The last zoea changes to the megalopa, which, instead of swimming with its maxillipedes, uses its pleopods, now provided with long setæ, the abdomen being held out horizontally and the maxillipedes functioning as mouth-parts. The body is flattened dorso-ventrally. The third maxillipede is fully developed and all the legs, the form being crab-like except for the fact that the abdomen is not normally curled under the body, although this can now be done.

In none of the British species studied is there more than one megalopal stage, and this changes directly into a crab. Cano has described two megalopal stages in several cases. It may be the fact that some foreign crabs have two, but in those he describes (*Pilumnus*, *Gonoplax*), which are also British species, there must be some mistake. The explanation seems to be that the megalopa certainly grows, and has a different appearance when first emerging from the zoeal skin. When ready to cast its skin, it looks more like the crab, which shows through the megalopal covering. It is to be noted also that Cano's (1890) specimens of the megalopa, which he regards as *Gonoplax*, do not belong to that genus, but probably to *Cancer* or *Pirimela*. The megalopæ may be distinguished from one another by the following characters:—Form of rostrum or front of carapace. Presence or absence of median dorsal spine on carapace, or other spines and prominences. Presence or absence of feelers on last legs. Number of setæ on last pleopods. Number of hooks on legs.

The rostrum is absent in *Ebalia* and in *Pinnotheres veterum* (probably in the other species of *Pinnotheres*), where the carapace has merely an undulating front margin slightly protruding in the centre (Pl. XII. fig. 9; Pl. XIII. figs. 8, 10). In all the other British crabs where the megalopa is known there is a rostrum. This has one spine in *Portunus* (Pl. V. fig. 1), *Portumnus* (Pl. VIII. fig. 1), *Carcinus* (Pl. VII. fig. 4), *Pirimela* (?) (Pl. VII. fig. 6), *Cancer* (Pl. X. fig. 3), *Atelecyclus* (Pl. IX. fig. 5), *Thia* (Pl. VIII. fig. 8), *Pilumnus* (Pl. X. fig. 6); and *Maia* (Pl. XIV. fig. 6) is almost square in *Gonoplax* (Pl. XII. fig. 3), two-horned in *Inachus* (Pl. XV. fig. 2), three-toothed in *Hyas* (Pl. XIV. fig. 9) and *Corystes* (Pl. XIII. fig. 2), square with a central prolongation and a spine at each angle in *Xantho* (Pl. XI. fig. 8), and bluntly trilobed in *Macropodia* (Pl. XVI. fig. 1). In many forms it is turned down at an angle so that the central spine hardly shows, or it may stick out horizontally. There is a dorsal spine on the carapace in *Hyas*, *Corystes*, *Cancer*, *Atelecyclus*, and *Pirimela* (?); and there are several extra spines in *Macropodia* and *Inachus*, two spines in front in *Gonoplax*, conspicuous knobs in the Portunidæ, *Xantho and Pilumnus*, inconspicuous knobs in *Ebalia* (Pl. XIII. fig. 10) and *Pinnotheres* (Pl. XII. fig. 9), and a smooth carapace in *Thia*. There are usually hooks on some of the legs ventrally on the coxæ and ischia and sometimes on the other joints, which are described under the various forms. Feelers in the shape of coarse curved setæ are present on the last joint of the legs in all the Brachyrhyncha studied, and this seems to be a distinct feature of that group. In the Pinnotheridæ (Pl. XII. fig. 9) alone are these absent. They are, however, absent in all the Oxyrhyncha (Pl. XVI.) and in *Ebalia* (Pl. XIII. fig. 8). The number of setæ on the last pleopods is usually constant for the species, forming good distinguishing characters. The carapace of *Corystes* is exceptional in having lateral teeth.

It is possible, from the details given above, to recognize the megalopa of every British genus where it is known, and now only those of *Pisa* and *Achæus*, in the Oxyrhyncha, and *Polybius* and *Bathynectes*, in the Brachyrhyncha, remain to be discovered. The presence of feelers on the last joint of the last legs cuts off the Brachyrhycha (with the exception of the Pinnotheridæ) from the Oxyrhyncha and from *Ebalia*, so that two natural groups are formed, *Pinnotheres* and *Ebalia* remaining outside.

It seems impossible to find anything primitive in a megalopa, which is decidedly a very specialised larva, present in almost all crabs, but the characters do fit in well with those of the zoeæ so that a natural classification may be arrived at, which, with a few exceptions, agrees well with the existing classification of the adults.

Thus, as before, taking the Brachyrhyncha as the most primitive, we have, going with the group, the presence of feelers on the last legs. It is possible that this may be a device for cleaning the branchiæ, but so far no special function has been detected, and it is difficult to see why, if this were the case, it should not be wanted in the other groups. A key to the megalopæ is given in order to identify the genera.

Key to the Megalopæ.

I. No feelers on last joint of last leg.

  1. Rostrum absent.

    a. Six abdominal segments, including telson . ... *Pinnotheres* (*P. veterum* only known).

    b. Seven abdominal segments, including telson . . .. *Ebalia.*

  2. Rostrum present.

    a. One dorsal spine on carapace, rostrum three-toothed... *Hyas.*

    b. Several dorsal spines on carapace. Six abdominal segments only, including telson.

      α. Dorsal spines long; rostrum bent down, forming three lobes .... *Macropodia.*

      β. Dorsal spines short; rostrum two-horned, sticking out horizontally. .... *Inachus.*

    c. No dorsal spines on carapace, but rounded protuberances; broad rostrum bent down, almost hiding a central spine

      α. Rostral spine large and pointed; 3 setæ on last pleopods .... *Eurynome.*

      β. Rostral spine sharp and small; 5 setæ to last pleopods .... *Maia.*

II. Feelers on last joint of last legs.

  . Dorsal spine on carapace.

    α. Rostrum with 3 spines. Lateral spines to edge of carapace .... *Corystes.*

b. Rostrum finely pointed, not bent. No lateral spines on edge of carapace.
α. Dorsal spine of carapace sticking out horizontally behind.
× 10 setæ to last pleopods... . .. .. . *Atelecyclus*.
×× 8 setæ to last pleopods . . .. *Cancer*.
β. Dorsal spine hook-like, sticking up from near centre of carapace; 7 setæ to last pleopods .. . .. *Pirimela* (?).
2. No dorsal spine to carapace.
a. Rostrum square or squarish.
α. Rostrum square, without spines ... . *Gonoplax*.
β. Rostrum squarish, with spine at the outer angles and a central bent protuberance .. . . *Xantho*.
b. Rostrum pointed.
α. Carapace smooth .... *Thia*.
β. Carapace with knob-like protuberances.
× Protuberances very conspicuous ... . *Pilumnus*.
×× Protuberances not conspicuous.
○ 5 setæ to last pleopods .... *Carcinus*.
○○ More than 5 setæ to last pleopods ... . *Portunus* (including *Portumnus* and probably *Bathynectes* and *Polybius*).

METHODS OF REARING.

The crabs were reared in plunger-jars, aërated aquaria, and small bowls, the plunger-jars in which three species were reared from egg to crab proving the best. The most effective food was oyster larvæ taken from the parent oyster when ready to swim. The larvæ pipetted out into the aquarium, scattered themselves all over the jar, and were eaten by the zoeæ. Other larvæ given and eaten were *Pomatoceros* larvæ, *Echinus* larvæ, and *Teredo* larvæ from artificial fertilisations. Crab eggs were eaten, but no larvæ were reared on these and the later zoeæ ate smaller zoeæ. *Inachus* zoeæ were seen to eat very young herrings, which were hatched from the egg in the same jar. No larvæ were reared on a purely vegetable diet, although the most successful experiments were in jars containing green algæ and diatoms as well as the animal food. *Pinnotheres pisum* fed well on *Nitzschia* when in the first zœal stage, but never shed their skins. The megalopæ were fed on small pieces of the mantle of the common mussel, *Mytilus edulis*, and the small crabs also ate this and grew. The crabs reared from the egg were fed on oyster larvæ from the first to the last zoea and on mussel from the megalopa through the crab stages. One crab, *Portunus puber*, is still alive, aged six months and in the ninth crab stage. Zoeæ and megalopæ from the plankton were fed in the same way.

The following is a list of all crabs reared through any stage:—

From egg to 9th crab stage	*Portunus puber.*
„ „ 7th „	*Inachus dorsettensis.*
„ „ 1st „	*Xantho incisus.*
„ „ megalopa	**Inachus dorynchus.*
„ „ „	**Maia squinado.*
„ „ „	**Macropodia longirostris.*
„ „ „	**M. rostratus.*
„ „ last zoea	**Inachus leptocheirus.*
„ „ „	**Macropodia egyptia.*
„ „ „	**Eurynome aspera.*
„ „ „	**Pilumnus hirtellus.*
„ „ „	**Carcinus mænas.*
„ „ third zoea	**Cancer pagurus.*
„ „ „	**Portunus depurator.*
„ „ second zoea	**P. pusillus.*
„ „ „	**P. holsatus.*
„ „ „	**P. marmoreus.*
„ „ „	**Atelecyclus septemdentatus.*
„ „ first zoea	**Ebalia tuberosa.*
„ „ „	**Hyas coarcticus.*
„ „ „	*Xantho hydrophilus.*
„ „ „	*Portunus corrugatus.*
„ „ „	** P. arcuatus.*
„ „ „	*Bathynectes longipes.*
„ „ „	*Polybius henslowi* (from
„ „ „	*Pinnotheres pisum.* [Mr. Todd).

Larvæ from the Plankton:—

First zoea to megalopa and crab	*Corystes cassivelaunus.*
„ „ „	*Gonoplax rhomboides.*
Second „ „	*Thia polita.*
„ „ only	*Pinnotheres veterum.*
Last „ and crab	*Pirimela denticulata* (?).
First zoea to last zoea (megalopa from last zoea)	*Ebalia cranchii.*
Megalopa (crab from megalopa)	*Portumnus biguttatus* (from
Larvæ not seen at all	*Achæus cranchii.* [Mr. Gurney).
	Pisa biaculeata.
	Hyas araneus.
	Ebalia tumefacta.

* Crabs marked * show that the rest of the life-history was finished from the plankton, and the crabs reared from the megalopæ.

The Plymouth crabs are given below arranged according to Borradaile's (1907) classification. Whilst the larval forms, for the most part, fit in very well with this classification, closely-related forms usually having definitely related larvæ, there are certain outstanding anomalies which should be mentioned. As an example of a naturally related group we may take the Portunidæ, the larvæ of which agree in every essential, so that it would be possible to pick out a Portunid larva in any stage. Again, *Xantho* agrees very well with some of the foreign Xanthidæ larvæ recently described, and we could easily recognize a relative. Any of the Inachinæ can be distinguished at a glance, and one of the Oxyrhyncha can be separated from one of the Brachyrhyncha at any stage. The greatest puzzle is the close resemblance between some of the Pinnotheridæ and Leucosiidæ. Now, the Pinnotheridæ are placed, and apparently rightly, in the Brachyrhyncha, being presumably closely related to the Grapsidæ. This is borne out by Hyman's (1925 *a* and *b*) recent descriptions of the larvæ of *Planes* and of the Pinnotheridæ. *Planes* links up well with *Pinnotheres* through *Dissodactylus*. Unfortunately, we do not know the megalopæ of any of these except the Plymouth *Pinnotheres veterum*, but the zoeæ are clearly related in this sequence. *Ebalia* belongs to the Leucosiidæ, and is the only British representative of the family and of the Oxystomata. Gurney (1927) figures zoeæ of *Leucosia* from the Red Sea, and these are very like *Ebalia*, but also one of them is strikingly like *Pinnotheres pisum*. The only other larval oxystomes known are the very peculiar *Dorippe* and *Ethusa*, which are extremely unlike *Ebalia* and *Leucosia*. On examining the *Ebalia* larvæ we find they resemble those of *Pinnotheres pisum* very closely in the zoeæ, and the megalopa resembles that of *P. veterum*, the megalopæ having in common two characters so far not found in the Brachyrhyncha—the absence of rostrum and of feelers on the last legs. The latter character is shared by the Oxyrhyncha. The only explanation at all reasonable for the likeness in the zoeæ is their common adaption to a life near the bottom instead of near the surface, but this does not explain the megalopal characters, and the facts remain a puzzle.

Cunningham (1891) has shown clearly that *Atelecyclus* is very closely related to *Cancer*. This is abundantly proved by its larval forms, which resemble one another in almost every important particular. *Pirimela*, usually placed in the Cancridæ, is, if my identification of the larvæ be correct, more closely related to the Portunidæ, especially to *Carcinus*, but differs from all enough to place it in a family of its own. *Thia*, which is usually placed with *Atelecyclus*, differs very considerably in the larva, and should, I think, be placed in a separate family near *Corystes*, both being near the Cancridæ. Amongst the Spider-Crabs *Eurynome* is very like *Maia* in its larva, and not like the larvæ of the Parthenopidæ described by Cano, whilst from the descriptions of *Pisa* by Cano and Gourret it should be closely related to *Inachus* and not to to *Hyas*. The following arrangement is suggested as showing best the larval affinities. It remains for the future to show whether the innovations are justified.

BRACHYRHYNCHA.

- Family PORTUNIDÆ.
    - Subfamily *PORTUNINÆ.*
        - Genus PORTUNUS.
        - BATHYNECTES.
        - POLYBIUS.
    - Subfamily *CARCININÆ.*
        - Genus CARCINUS.
    - Subfamily *PORTUMNINÆ.*
        - Genus PORTUMNUS.
- Family PIRIMELIDÆ.
    - Genus PIRIMELA.
- Family CANCRIDÆ.
    - Subfamily *CANCRINÆ.*
        - Genus CANCER.
    - Subfamily *ATELECYCLINÆ.*
        - Genus ATELECYCLUS.
- Family CORYSTIDÆ.
    - Genus CORYSTES.
- Family THIIDÆ.
    - Genus THIA.
- Family XANTHIDÆ.
    - Subfamily *XANTHINÆ.*
        - Genus XANTHO.
    - Subfamily *MENIPPINÆ.*
        - Genus PILUMNUS.
- Family GONOPLACIDÆ.
    - Genus GONOPLAX.
- Family PINNOTHERIDÆ.
    - Genus PINNOTHERES.

OXYSTOMATA.

- Family LEUCOSIIDÆ.
    - Genus EBALIA.

OXYRHYNCHA.

Family MAIIDÆ.
  Subfamily *MAIINÆ.*
    Genus MAIA.
      EURYNOME.
  Subfamily *PISINÆ.*
    Genus HYAS.
      PISA (?).
  Subfamily *INACHINÆ.*
    Genus INACHUS.
      MACROPODIA.
      ACHÆUS.

The Oxystomata have been placed between the Brachyrhyncha and the Oxyrhyncha to show the resemblances to both. In support of their likeness in some ways to the Brachyrhyncha, we have Garstang's (1897) suggestions as to the Oxystomata being possibly derived from the Portunidæ.

A comparison of the suggested classification given above with the list of Plymouth crabs arranged according to Borradaile given below is interesting, for whilst the larval characters in some groups fit in well with his classification, in others a different arrangement seems necessary.

THE PLYMOUTH BRACHYURA ARRANGED ACCORDING TO BORRADAILE'S CLASSIFICATION.

Tribe **BRACHYURA.**
  Sub-Tribe **BRACHYGNATHA.**
    Superfamily BRACHYRHYNCHA.
      Family CORYSTIDÆ.
          Genus CORYSTES.
            Corystes cassivelaunus (Pennant).
      Family ATELECYCLIDÆ.
        Subfamily *ATELECYCLINÆ.*
          Genus ATELECYCLUS.
            Atelecyclus septemdentatus (Montagu).
        Subfamily *THIINÆ.*
          Genus THIA.
            Thia polita Leach.

Family CANCRIDÆ.
  Subfamily *CANCRINÆ.*
    Genus CANCER.
      Cancer pagurus L.

Family PIRIMELIDÆ.
    Genus PIRIMELA.
      Pirimela denticulata (Montagu).

Family PORTUNIDÆ.
  Subfamily *CARCINIDINÆ.*
    Genus CARCINUS.
      Carcinus mænas Penn.
  Subfamily *PORTUMNINÆ.*
    Genus PORTUMNUS.
      Portumnus biguttatus (Risso).
  Subfamily *PORTUNINÆ.*
    Genus PORTUNUS.
      Portunus puber (L.).
        corrugatus (Penn.).
        arcuatus Leach.
        pusillus Leach.
        marmoreus Leach.
        holsatus Fabricius.
        depurator (L.).
    Genus POLYBIUS.
      Polybius henslowi Leach.
    Genus BATHYNECTES (Risso).

Family XANTHIDÆ.
  Subfamily *XANTHINÆ.*
    Genus XANTHO.
      Xantho incisus Leach.
        hydrophilus (Herbst).
  Subfamily *MENIPPINÆ.*
    Genus PILUMNUS.
      Pilumnus hirtellus (L.).

Family CARCINOPLACIDÆ.
    Genus GONOPLAX.
      Gonoplax rhomboides (L.).

- Family PINNOTHERIDÆ.
  - Genus PINNOTHERES.
    - *Pinnotheres pisum* (Penn.).
      - *veterum* Bose.

Superfamily OXYRHYNCHA.

- Family PARTHENOPIDÆ.
  - Subfamily *PARTHENOPINÆ.*
    - Genus EURYNOME.
      - *Eurynome aspera* (Penn.).
- Family MAIIDÆ.
  - Subfamily *INACHINÆ.*
    - Genus INACHUS.
      - *Inachus dorsettensis* (Penn.).
        - *dorynchus* Leach.
        - *leptocheirus* Leach.
    - Genus MACROPODIA.
      - *Macropodia longirostris* (Fabricius
        - *rostratus* (L.).
        - *egyptia* A. M.-Edwards.
    - Genus ACHÆUS.
      - *Achæus cranchii* Leach
  - Subfamily *PISINÆ.*
    - Genus PISA.
      - *Pisa biaculeata* (Montagu).
    - Genus HYAS.
      - *Hyas araneus* (L.).
        - *coarctatus* Leach.
    - Genus MAIA.
      - *Maia squinado* (Herbst).

Sub-Tribe **OXYSTOMATA.**

- Family LEUCOSIIDÆ.
  - Subfamily *LEUCOSIINÆ.*
    - Genus EBALIA.
      - ***Ebalia tuberosa*** (Penn.).
        - ***tumefacta*** (Montagu).
        - ***cranchii*** Leach.

PREVIOUS WORK ON THE LARVAL BRACHYURA.

There has been little detailed work on larval crabs, chiefly because of the difficulty in rearing them. Some of the earliest naturalists hatched out the eggs and obtained pre-zoeæ and zoeæ. The first to understand that these were actually crab larvæ was E. V. Thompson (1829), who hatched out *Cancer pagurus*. He was so little credited that for several years it was not universally believed. Before that time many larval forms were regarded as separate genera, Montague (1804) and Leach (1815) naming and describing several larvæ in this way under the generic name of *Megalopa*. Du Cane (1839) was the first to realise the true nature of the pre-zoeæ in *Carcinus*. Many other naturalists later hatched out other zoeæ:—Goodsir (1842), Kinahan (1846). Couch (1843) hatched out several and (1853) reared *Cancer* to the megalopa. Bell (1853) mentions several workers who had hatched out the larvæ, but hardly any consecutive life-histories were followed up. Spence-Bate (1858), by collecting the larval stages from the plankton, described fairly accurately the whole of the life-history of *Carcinus mænas*. Although this account is extremely valuable because of its containing so much that is new, it is not entirely to be relied on, as was pointed out by several workers a little later. Brook (1884) gives accurate drawings of the megalopa and young stages of the same species. Claus (1876) describes and figures several crab larvæ, and from this time onwards there has been a continuous stream of work on larval crabs. Of these, Faxon (1879–80), Conn (1884–87), and Smith (1873–82) in America made important additions to our knowledge and studied the first zoeæ and embryonic cuticle. Gourret (1884) hatched out some larvæ at Marseilles, and Cano (1888–92), whose work is of the greatest importance, published a series of papers on the various stages and relationships of the larvæ of the Mediterranean crabs, both zoeæ and megalopæ, and also their embryology and young crab stages. Many of these are still the only descriptions available of certain species; but although hatching several from the egg, Cano did not succeed in rearing them, and therefore was obliged to make up the gaps in the life-histories from the plankton. It necessarily followed that many stages were omitted and others were not correctly identified. Gurney (1903) describes the life-history of *Corystes cassivelaunus* from Plymouth, like Cano, picking out the different stages from the plankton. He also describes the pre-zoea and zoea of *Eurynome* (1924 *a*), and has recently made some very interesting suggestions (1924–27) as to the significance of the embryonic cuticle. His monographs on the decapod larvæ of the 'Terra Nova' and the Cambridge Suez Canal Expeditions describe some interesting zoeæ (1925–27). Pearson (1908), in his work on *Cancer pagurus*, states that he was unable to rear the larvæ, and only figures it as far as the first zoea. Williamson (1900–1915) also describes these early stages, and in a series of papers culminating in his survey of the decapod larvæ in 'Nordisches Plankton' he gives accounts of several zoeæ and megalopæ of the British crabs, not, however, succeeding in rearing any species through its various stages. Miss Jorgensen (1918) reared *Carcinus mænas* from egg to megalopa in aërated aquaria at Cullercoats, and describes the life-history of an *Ebalia* (1923). Schlegel (1911) was apparently the first and only worker to rear any crab through all its larval stages to the crab. At Roscoff he succeeded in rearing *Maia squinado* from egg to young crab. Unfortunately, he does not describe his methods or give any figures. Björk (1913) describes the life-history of *Portunus depurator* from the plankton, but did not rear it, and various authors have described zoeæ and megalopæ of different crabs from plankton samples up to the present time. Of these, the most important are by Conolly (1913–14) and Hyman (1920–27), the first describing the life-history of the American crabs *Cancer amœnus* and *Rhithropanopeus harrisi*, the second publishing several accounts of the larvæ of certain families—Pinnotheridæ, Grapsidæ, and Xanthidæ—besides a separate paper on *Gelasimus*. These are all valuable additions to our knowledge of crab larvæ, but they are nearly all from plankton samples, except for the first stages, many of which were hatched from the egg. In very rare cases these were reared to a stage or two later. Up to the present time there are clearly very few accounts of any crabs reared through many larval stages. In 1927 I published an account of *Inachus dorsettensis*, *Macropodia longirostris*, and *Maia squinado* reared from egg to megalopa, the young crabs being reared from megalopæ collected from the plankton. Later (1928) a short paper was published on the larval stages of *Ebalia* and *Pinnotheres*. The present work shows further progress in that three species have been reared from egg to crab, several more to the megalopa, and many others through various zoeal stages.

HABITS OF THE CRAB LARVÆ.

The pre-zoeæ and zoeæ nearly always tend to move towards the surface and light. Directly the eggs hatch the pre-zoea wriggles upwards, and in an aquarium is easily removed by a pipette. With the exception of the zoeæ of *Ebalia* and *Pinnotheres*, which habitually curl up in balls, the zoea also moves upwards and towards the light. The megalopa, although often coming up to the top, is more frequently seen near the bottom. The long spines of the carapace are mainly for helping in directing the movements of the zoea (Wheldon 1889), but also help in keeping it up together with the other outgrowths of the body. telson, abdominal spines, and antennæ; whilst the first and second maxillipedes are used for swimming, the outspread setæ forming a broad surface with which to beat the water, the abdomen being brought under the body and out again. Gurney (1903) draws attention to the fact that the long spines are present before the auditory organs are functional, disappearing in the megalopa when that organ begins to be of use. As the larva grows and the later zoeal stages are reached, the body is heavier and more setæ appear on the swimming-maxillipedes, long spines usually growing out from the abdominal segments.

In the plankton taken from outside the Breakwater, from near the bottom to the surface, the larval crabs occur at all depths, but frequently are not so abundant in the actual surface-layers as in those lower down. This fact is borne out by Russell's researches on the vertical distribution of marine macroplankton (1927). He states " it will be noticed that while, usually, they avoided the actual surface-layers, they were frequently numerous right up within 5 metres of the surface." He found, however, that *Ebalia* was absent above 20 metres. Nearer inshore, however, it comes into shallower water, although always preferring to be near the bottom. Savage (1926) finds *Portunus* in the upper layers. Russell found that there was a tendency for the megalopæ of all crabs to be slightly deeper in the water than the zoeæ. Swarms of one species frequently occur—*Corystes* in the spring, *Portunus* in the summer are often seen in enormous numbers, and sometimes *Inachus* and *Macropodia* in spring or autumn. *Carcinus*, although very common in the Sound, seems to scatter itself more, although at times many may be seen together. The first young crab stages of *Portunus* sometimes occur in large numbers in the plankton. Very young *Carcinus*, from about the second young crab stage, may be found along the shore among stones, and also *Portunus puber* at very low tide. Cunningham (*op. cit.*) also found *Cancer pagurus* in the first young stages under stones at low tide. No doubt with careful search other species would be found. A list of the breeding crabs, so far recorded, is given at the end of this section.

The natural food of the crab zoeæ consists of planktonic organisms—diatoms and probably other microscopic plants, and small animals, chiefly larval forms. The stomach usually contains débris also, which seems to be collected by the larva with the living food, chewed up, and swallowed. The larvæ of oysters and other molluscs, worms, and echinoderms are apparently natural food, and quite small zoeæ have been seen to eat them, smashing up the mollusc shells and echinoderm spines with their powerful mandibles whilst holding the food partly with the other mouth-parts and partly with the abdomen curled in under the body. Crab eggs are also eaten, and often the older zoeæ and megalopæ will eat one another, swimming about whilst sucking at the dead body, often nearly as large as themselves. Very small zoeæ, such as *Pinnotheres pisum* and *Ebalia*, were seen to eat diatoms (*Nitzschia*), but it is probable that the zoeæ as a rule do not grow on a purely vegetable diet, a mixture of animal and vegetable being the ideal food. The megalopæ will eat quite large crustacea, but thrive perfectly on pieces of mollusc or crustacean muscle. It is robable that they eat dead food in the sea. The young crabs eat the same sort of food as the megalopæ, but probably usually feed on bottom forms or dead matter.

Certain crabs mask themselves with any foreign matter available directly they come out of the megalopal skin. This is not surprising in the Spider-Crabs, which decorate themselves throughout their life; but it was found that *Cancer*, *Atelecyclus*, *Thia*, *Xantho*, and *Pilumnus* all had a tendency to do this, although the swimming crabs did not attempt to do so. *Cancer* and *Atelecyclus* continued to cover their bodies up to the third and fourth young stages, after which they usually ceased. Possibly the very young are so helpless that it is a great advantage to hide instead of running away. The swimming crabs being able to swim beautifully almost directly they emerge from the megalopa, do not need to cover themselves in this way.

The usual time for reaching the first crab stage seems to be about three weeks to a month, judging from rearing experiments. In natural surroundings it may be less. After the first crab stage the skin is cast about once a week for the first month, after which there are longer intervals, until at about four months old it begins to change about once a month or more. Temperature seems to affect them, for in the winter the changes were very slow.

The following list shows the breeding-time of the Plymouth crabs:—

List of Crabs in Berry and Occurrence of Larva.

Portunus puber	Berried crab chiefly in spring, rarely through the summer and as late as November. Larvæ in plankton April to August, rarely in autumn. Chiefly April to June.
P. corrugatus	Berried crab April, May, June. No larvæ seen in plankton.
P. arcuatus	Berried crab from April to August. Larvæ in plankton in spring and summer.
P. pusillus	Berried crab from April to July. Larvæ in plankton in spring and summer.
P. marmoreus	Berried crab from May to July. Larvæ in plankton in spring and summer.
P. holsatus	Berried crabs from April to July. Larvæ in plankton in spring and summer.
P. depurator	Berried crab March to October, occasionally in winter. Larvæ in the plankton chiefly in spring and summer.
Bathynectes longipes	Berried crab in July. Larvæ not seen in plankton.
Polybius henslowi	Berried crab in September 1898 (Mr. Todd).
Portumnus biguttatus	Berried crab in August (Mr. Todd). Megalopa in August (Mr. Gurney).
Carcinus mænas	Berried crab from December to November, chiefly February and March. Larvæ in plankton all the year round, chiefly spring.
Pirimela denticulata	Berried crab February to April (Mr. Todd). (?) Larvæ in plankton late summer and autumn.
Cancer pagurus	Berried crab in spring. Larvæ in plankton April to August.

Atelecyclus septemdentatus	Berried crab February to April, rarely in autumn. Larvæ in plankton March to June.
Corystes cassivelaunus	Berried crab April, July. Larvæ in plankton March to June. Rarely later.
Thia polita	Berried crab not seen. Larvæ in plankton August to October.
Xantho incisus	Berried crab March to July. Larvæ in plankton in spring and summer.
X. hydrophilus	Berried crab March to April, rare. No larvæ seen in plankton.
Pilumnus hirtellus	Berried crab April to August. Larvæ in plankton in spring and summer.
Gonoplax rhomboides	Berried crab in June (Mr. Todd). Larvæ hatched. Larvæ in plankton August, September.
Pinnotheres pisum	Berried crabs in June to August, rarely later. Larvæ in plankton in late summer.
P. veterum	No berried crabs seen. Larvæ in plankton August to October.
Ebalia tuberosa	Berried crab March to July. Larvæ in plankton January to October.
E. cranchii	Berried crab in April. Larvæ in the plankton in summer and autumn.
E. tumefacta (?)	No berried crab seen. Larvæ in the plankton in October (?).
Maia squinado	Berried crabs from May to October, chiefly July and August. Larvæ in the plankton in summer and autumn.
Eurynome aspera	Berried crabs in spring and summer. Larvæ in the plankton April to October.
Hyas coarctatus	Berried crabs April to August. Larvæ in the plankton in spring.
H. araneus	No berried crabs seen. No larvæ seen in the plankton.
Inachus dorsettensis	Berried crab all the year round. Larvæ in the plankton all the year round.
I. dorynchus	Same as *dorsettensis*.
I. leptocheirus	Same as *dorsettensis*.
Macropodia longirostris	Same as *Inachus*.
M. rostratus	Berried crabs all the year round, but rare in winter. Larvæ in the plankton chiefly in summer and autumn.
M. egyptia	Berried crabs in spring and summer. Larvæ probably common in the plankton, but difficult to distinguish from *M. rostratus*.
Pisa biaculeata	Berried crab July. No larvæ seen in the plankton.
Achæus cranchii	Berried crab in March (Mr. Hunt). No larvæ seen in the plankton.

SYSTEMATIC PART.

The BRACHYRHYNCHA.

The following characters of the larvæ apply to all the British forms excepting the Pinnotheridæ. Few foreign forms have been described completely, but those which are certainly known agree, except in a few details, with the present diagnosis :—

Pre-zoeæ with the usual seven embryonic spines each side on the telson, the seventh usually non-hairy, two on the antennules, one much shorter than the other, and three or four on the antenna covering the exopodite, with a simple sheath for the spinous process.

Four or five zoeal stages having typically 4, 6, 8, 10, 12 setæ on the maxillipedes in the respective stages. Those with four zoeal stages have 10 in the last stage and those with five have 12 in the last stage (*Corystes* is exceptional in having 10 in the third, 12 in the fourth, and 14 in the fifth). Antenna of zoea with well-developed exopodite and spinous process. First and second zoeæ backward in development, the antennal flagellum, pleopods, and long lateral spines on the abdominal segments usually not appearing until the third stage. Telson forked. Five abdominal segments plus telson in the first and usually in the second stage, six plus telson in the later stages.

Megalopa with rostrum straight or bent, with feelers on the last joint of the last legs.

The Pinnotheridæ, as represented by *Pinnotheres*, differ in having rudimentary antennæ in all zoeal stages and in having only five abdominal segments in both zoeæ and megalopa. The number of zoeal stages varies, *Pinnotheres veterum* having two only, the second (last) having six setæ on the maxillipedes, the first zoea being far advanced in development, whilst *P. pisum* is not nearly so advanced, and probably has three or four zoeal stages. Both the British species have a peculiar three-lobed telson separating them from all the other crab zoeæ. Some foreign species may, however, have a typical forked telson. Megalopa without rostrum and without feelers on the last joint of the last legs.

Key to the Genera of the Brachyrhyncha (British).

ZOEÆ.

I. Telson three-lobed .... *Pinnotheres.*

II. Telson forked.

1. No lateral spines on carapace.

   a. From tip of dorsal to tip of rostral spine about body-length . *Carcinus.*

   b. From tip of dorsal to tip of rostral spine longer than body-length .... *Pirimela* (?).

2. Lateral spines present.

   a. Antennal exopodite rudimentary .... *Xantho.*

   b. Antennal exopodite as long as or nearly as long as the spinous process.

      × Knobs on abdominal segments 2 to 4 or 5 .... *Gonoplax.*

      ×× Knobs on abdominal segments 2 and 3 only .... *Pilumnus.*

   c. Antennal exopodite from a third to two-thirds the length of the spinous process, ending in spines.

      × One lateral spine on telson.

         ○ Rostral spines more than two-thirds the length of the dorsal spine .... *Corystes.*

         ○○ Rostral spine less than two-thirds the length of the dorsal spine .... *Thia.*

×× Two lateral spines on telson.

◎ Antennal exopodite one-third the length of the spinous process ... ... *Cancer.*

◎◎ Antennal exopodite one-half to two-thirds the length of the spinous process .... *Atelecyclus.*

××× Three lateral spines to telson. *Portunus* (except in later stages of *P. puber*, where they are reduced to two), including *Bathynectes* and *Polybius.*

MEGALOPÆ.

I. No feelers on last joint of last legs................ .... *Pinnotheres.*

II. Feelers on last joint of last legs (see General Key to Megalopæ).

Family PORTUNIDÆ.

Pre-zoeæ with three long spines on the antenna, the seventh long spine on the telson usually without hairs. Four or five zoeal stages. Dorsal and rostral spines on the carapace; laterals usually present. Antenna with exopodite ending in spines, about half as long as the spinous process. Telson with three lateral spines usually in all stages, but they may dwindle in the later stages in some species to two or one. Usually one or two extra internal pairs of setæ in the later stages. Lateral spines usually on third to fifth abdominal segments in the later stages. Second and third abdominal segments each with a pair of lateral knobs; those on the second hook-shaped. Those on the third segment disappear in the later stages. Four hairs dorsally on the first abdominal segment, two on segments 2 to 5. Megalopa with one-spined rostrum and no dorsal spine. Carapace with not very conspicuous prominences. Large hook on ischia of first leg, and usually hooks on coxæ of second to fourth legs. First young stage with three-lobed front to carapace more or less produced. Five teeth each side, the second and fourth smaller than the others. Last legs usually paddle-shaped.

Subfamily *PORTUNINÆ.*

Five zoeal stages. Lateral spines on carapace present. Telson with three lateral spines in all stages (except in *Portunus puber*, where one disappears in the later stages). One extra pair of internal spines in second, third, or fourth stage, two extra pairs in fourth or fifth stage. Lateral spines on third to fifth abdominal segments in later stages. Megalopa with rostral spine sticking out horizontally or bent; last pleopods with more than five setæ. Hook-shaped spines on second to fourth legs (Claus [1876] describes a spine on the fifth leg in *Portunus*, but there is none on this last leg, the spine on the fourth showing behind, as it appears in the drawing). First young crab with swimming-paddles on last legs.

The Plymouth genera belonging to the Portuninæ are *Portunus*, *Bathynectes*, and *Polybius*; the last two very rare, each being represented by one species only, *Portunus* consisting of seven species. Palmer (1927) regards *P. puber* as the most primitive. It is interesting that *P. puber* is the only species (the later stages of *P. corrugatus* not being known) which loses one of the lateral spines of the telson in the later stages, thus resembling in almost every particular similar stages in *Cancer* and *Atelecyclus*. It also has much longer rostral and dorsal spines than any of the other species, and is much more highly coloured, again bringing it near *Cancer*. The other species are rather like one another; indeed, so much so are the small species *P. pusillus* and *P. arcuatus* that it is very difficult, if not impossible, to tell them apart except after the most minute examination. It is difficult to recognize the later zoeæ of any of the others, as they tend to be much alike in colouring, and the megalopæ are nearly all coloured in the same way, *P. puber* included. Descriptions are given of all the species, but unless these are reared or taken alive in the plankton, it is not worth while trying to separate them. This also applies to *Bathynectes* and *Polybius*, which are exceedingly like *Portunus*, but, unfortunately, only known in the first zoea. It is practically impossible to recognize these amongst a collection of mixed portunids.

Previous work on the Portuninæ refers entirely to *Portunus*. The first zoea of certain species were hatched out by several of the old naturalists. Williamson (1911) was the first to describe any of the later stages. He obtained zoeæ hatched from the parent, and later stages from the plankton of *Portunus puber*, *P. depurator*, and *P. holsatus*. These he redescribes in 'Nordische Plankton' (1915). Some of the stages he kept until they became megalopæ and young crabs. Björk (1913) gives a good description and figures of *P. depurator* from the plankton. Cano (1892 *b*) had many years before given descriptions of certain species and figured the first zoea of *P. pusillus* but no later stages, and other figures of various zoea by different authors are to be identified as *Portunus*. Thus the main characters of a *Portunus*-larva were fairly well known, the number of zoeal stages being correctly given and the one megalopa stage, but no life-history from pre-zoea to crab has been completed until now, and the larvæ of *P. marmoreus*, *P. arcuatus*, and *P. corrugatus* are described here for the first time and the zoeæ and megalopæ of all the British species distinguished, with the exception of the later stages of *P. corrugatus*.

Genus PORTUNUS.

Carapace spines of moderate length, usually from tip of rostral to tip of dorsal spine equal to, or not much longer than, the body-length. Colour brownish-black chromatophores with yellow and red, or only black and yellow, the black chiefly in the intestinal region and ventrally along the abdomen. Eyes usually with a blue glint flecked with yellow. Megalopa greenish, made up of black and yellow with a little red.

Portunus puber having been reached from egg to crab is detailed as a type of *Portunus*. It is, however, not altogether typical, as it loses one of the lateral spines of the telson in the later stages, whilst they all remain in the other species.

PORTUNUS PUBER (L.). (Pl. I. fig. 1; Pl. IV. figs. 1–4; Pl. V. figs. 1–4.)

The "Velvet Swimming Crab" is very common in the district both between tide-marks under stones and below low-water mark, and is even trawled beyond the Breakwater. Zoeæ occur abundantly in the plankton in spring and summer, and megalopæ in the summer. The spring is the best time for the zoeæ. Young crabs from about the fourth or fifth young stage are found under stones between tide-marks. Berried crabs occur from March to July and are even taken in November, but are most abundant in spring. These were placed in an aquarium tank until the eggs hatched out into pre-zoea, which were pipetted off into a plunger-jar, in which they were reared as far as the megalopa. The megalopa was then placed in a small bowl until it changed into a crab. After four moults the small crab was again transferred to a plunger-jar, in which it still lives, aged six months and measuring about three-quarters of an inch across. The zoeæ were fed on oyster larvæ, the megalopæ and young crabs on bits of mussel. The zoeæ also ate the larvæ of *Echinus*, *Teredo*, and *Pomatoceros*, but throve best on the oysters.

Williamson (1911, 1915) obtained the first zoea from the berried crab, missing the pre-zoea. His description of the first zoea is adequate, but the later stages which he collected from the plankton might easily have been *Cancer pagurus*. This is suggested because the megalopa described and figured by him came from a fifth zoea and almost certainly belongs to *Cancer*. The form and coloration of the later zoeæ of *Cancer pagurus* and *Portunus puber* are very much alike, so much so that only an expert can tell them apart, and the description of the colour of the late zoea seems to agree better with *Cancer*, which is peculiarly brilliant and has more red and yellow and less black pigment than *P. puber*. The fact that his megalopa has a dorsal spine rules ont *Portunus* altogether, and the figure given is almost certainly the megalopa of *Cancer*. The first young stage figured by him is, however, truly a *Portunus*. Now, Williamson states that he was unable to see the dorsal spine in the cast megalopal skin from which this young came; therefore it is almost certain that in the specimen there was no dorsal spine, and that it was truly a *Portunus*. However, the first young stage figured (pl. iii. figs. 2–9; Williamson, 1911), although a *Portunus*, is not *P. puber*, for the central lobe is much too marked. Judging from the young of other species obtained from the megalopa, it is probably *P. pusillus* which has three pronounced lobes in front; the lateral teeth are as figured and are very similar to those of *P. puber*. All the first young crab stages from Plymouth, including those reared from the egg, had a markedly toothed front with a central lobe only slightly produced.

Portunus puber has the largest zoea and the longest and straightest spines of all the British portunids, and is also the most brilliantly coloured. It differs from the other species of which the life-history is known in losing one of the lateral spines of the telson in the later stages, a fact duly noted by Williamson. It may lose it in the second stage, or not until the fourth. Although the zoeæ are larger than the other species of *Portunus*, the megalopa is one of the smallest, and the first young stages are much smaller than those of *P. holsatus*, which is not nearly so large when adult. Williamson has rightly described the colouring of the zoea as reminding him of eosin. It is a brilliant pink on the dorsal and rostral spines and telson, with diffuse pink on the body and legs. There is also a good deal of pale yellow, especially in the front above the eyes and abdomen. A large amount of black occurs, black chromatophores in front of the dorsal spine, along the intestine, in the mouth-parts, above the maxillipedes, and ventrally along the abdominal segments. Dorsal and rostral spines long; longer than in the other species. In fact, as is stated above, it is easier to confuse it with *Cancer* than with the other species of *Portunus*. The megalopa has very little red about it, the general colour being green made up of black and yellow chromatophores, with blue eyes. It is very like the other *Portunus* megalopæ and has no trace of a dorsal spine. Thus in the early zoeæ and megalopa it is easily recognizable as a *Portunus*, in the later zoeal stages being more like *Cancer*.

Eggs a deep brown, changing to nearly black when ready to hatch. Early eggs about 0·38 mm., later eggs 0·44 mm. across. They are carried for several months, no exact data being obtained.

Pre-zoea about 1·76 mm. in length, without the embryonic spines, the characteristic colour of the zoea showing through the pre-zoeal skin. This lives for several hours, finally casting its skin and freeing the zoea.

First zoea about 1·76.* mm. in length; from tip of dorsal to tip of rostral spine about 2·24 mm. Thus the measurement from spine to spine is rather more than the body-length and greater than in any other *Portunus* species. Dorsal and rostral spines nearly straight, the dorsal slightly curved. Telson long. Sides of abdominal segments slightly toothed behind. Carapace edge with a few irregular serrations. Rudimentary third maxilliped and legs under carapace. Knobs on second and third abdominal segments.

Second zoea very like the first. Body-length about 2·24 mm. Length from spine to spine about 2·5 mm., length from spine to spine compared with body-length having decreased. Lateral

---

* All measurements of the body-length are taken from the front of the head to the tip of the telson fork.

outgrowths of abdominal segments 2 to 5 slightly longer. Knobs on third segment still present. Long hairs on outer edge of carapace. Three lateral spines still on telson, but in exceptional cases one, the middle one, may have disappeared. Still five abdominal segments plus telson.

Third zoea. Body-length about 2·5 mm. From spine to spine about 3 mm. Six abdominal segments plus telson. Knobs on third segment have disappeared. Long hairs on edge of carapace. Third maxillipedes and legs fairly prominent, but mostly hidden under carapace. Spines at sides of abdominal segments 3 to 5 appearing. Pleopods present as small projections. Antennal flagellum beginning. Telson may still have three lateral spines or the middle one may have disappeared. An extra pair of internal setæ inside fork usually present, but may not appear until the next stage.

Fourth zoea. Body-length about 3·8 mm. Length from spine to spine about 4 mm. Long hairs on edge of carapace. Rudimentary legs more developed. Spines on abdominal segments 3 to 5 longer. Pleopods and antennal flagellum longer. Only two lateral spines on telson. Usually two pairs of extra internal setæ, sometimes only one pair. Antennule swollen at base, with more spines and æsthetes.

Fifth zoea. Altogether heavier in build. Body-length about 4 mm. Length from spine to spine about 4 mm. Antennule jointed with branch. Antennæ with fairly long unjointed flagellum. Mandible with palp. Telson as in stage 4, with two pairs of extra internal setæ. Lateral spines on segments 2 to 5, long. Pleopods long, with branch. Long hairs on edge of carapace. Rudimentary third maxillipedes and legs much larger, the legs showing jointing, the first chelate and very heavy.

When the last zoea is ready to cast its skin the dorsal spine becomes hollow, and the remains of the living tissue contained in it descends and is seen as a red knob at the base of the spine. In the megalopa this remains as a slight prominence.

Megalopa small and greenish, quite unlike the zoea in colouring. Carapace 1·28 mm. long. Length from bending of rostrum to end of telson 3 mm. Protuberances on carapace inconspicuous. Rostrum finely pointed and bent down at an obtuse angle. Pleopods with many setæ, the last pair with ten only, rarely nine.

First Young Crab Stage brownish and speckled all over. Front of carapace with three indistinct lobes, denticulated in such a manner that one can recognize the species. Carapace nearly round, with five teeth each side, the second and fourth very small, the first and fifth prominent. Last legs ending in slender paddles. Breadth of carapace about 2·8 mm. in specimens reared from the egg. May be as small as 2·06 mm. in those reared from megalopæ from the plankton. Successive moults showed a carapace breadth of 2·06, 2·8, 4·48, 7·36, 9·60 mm.

The front grows more and more characteristically denticulated, the lateral teeth become large, notches in the orbit appear, and in the fifth stage the paddles are ridged. It is, by the fifth stage, quite definitely *Portunus puber*, with the carapace of the usual shape having grown steadily broader, and the colouring more or less like the adult.

The following data show the times taken for one *Portunus puber* to reach the tenth young crab stage:—

Pre-zoea from egg	23. 6.27
First zoea from pre-zoea	23. 6.27
Second zoea from first	28. 6.57
Third zoea from second	1. 7.27
Fourth zoea from third	4. 7.27
Fifth zoea from fourth	8. 7.27
Megalopa from fifth	12. 7.27
First young crab from megalopa ..	25. 7.27
Second young crab from first	1. 8.27
Third young crab from second	8. 8.27
Fourth young crab from third	17. 8.27
Fifth young crab from fourth	29. 8.27
Sixth young crab from fifth	7. 9.27
Seventh young crab from sixth ...	26. 9.27
Eighth young crab from seventh...	21.10.27
Ninth young crab from eighth ...	21.11.17
Tenth young crab from ninth	29.12.27 (died in casting skin).

It is thus seen that it takes just over a month to reach the first crab stage, later changes of skin usually taking longer, until there is a full month between stages 8 and 9 and over a month between stages 9 and 10.

PORTUNUS CORRUGATUS (Penn.). (Pl. I. fig. 2.)

The "Wrinkled Swimming Crab" is much less common in the district than it was some years ago. It occurs on the usual dredging and trawling grounds both inside and outside the Sound. Berried females from April to August, more commonly in spring. The larvæ have not been seen in the plankton, but two batches of eggs were hatched out in aquaria, and pre-zoea and first zoea obtained. These, unfortunately, did not live to cast their skins, and became second zoeæ. No description has hitherto been given of the larvæ.

Eggs reddish-orange, changing to a speckled brown when ready to hatch. Early eggs 0·32 mm., late eggs 0·4 mm. across.

Pre-zoea about 1·4 mm. long, soon changing to the first zoea.

First zoea about 1·7 mm. long; from spine to spine about 1·34 mm. Colour pinkish-grey, with a few black chromatophores chiefly under the abdomen and below the carapace. A small black chromatophore at the base of the dorsal spine. Eye blackish-blue splashed with yellow. The whole of the dorsal part of the body colourless. Dorsal and rostral spines curved, much shorter than in *P. puber*. These zoeæ were very delicate, would not eat, and soon died. Later zoea and megalopa not seen.

PORTUNUS ARCUATUS Leach. (Pl. I. fig. 3; Pl. VII. fig. 2.)

The "Arch-fronted Swimming Crab" is fairly common in the district, not far from the coast. Berried females April to September, chiefly in spring. Zoeæ and megalopæ common in the plankton in spring and summer. Eggs hatched in aquaria as pre-zoea, which soon changed to first zoea, but these did not live. Later zoeæ were obtained from the plankton and the megalopa, and young crab reared from these. It is very difficult to distinguish the zoeæ in the plankton, as they are much like many of the other *Portunus* species, the colour being variable and the sizes not very different. They are specially like *P. pusillus*, being very small in the early zoea, the smallest of all the *Portunus* species known. The later the zoeæ the more like the other species it becomes. It is really a waste of time trying to separate them in the plankton unless they are reared to the crab stages. This was done with most of the species, and the zoeæ and megalopæ distinguished. No description has hitherto been given of the larvæ of this species.

Eggs reddish, changing to almost black. Early eggs 0·26 mm., late eggs 3 mm. across.

Pre-zoea about 1·12 mm. long, soon changing to the first zoea.

First zoea about 1 12 mm. long. From spine to spine about the same. Colour yellowish, with black chromatophores along intestine, underside of abdomen, region of mouth-parts, and base of legs. Telson and spines of carapace colourless. Edge of carapace denticulated, changing to long hairs in the later stages. Dorsal and rostral spines curved. As the zoea grows the dorsal spine becomes yellowish, especially in the last stage. The changes in the zoea are very similar to those of *P. puber*, but the three lateral spines remain on the telson in all stages. The last zoea measures about 3 mm.; from spine to spine about the same. When about to change into the megalopa the living tissue of the dorsal spine descends as a yellow knob.

Megalopa obtained from the last zoea. Very like *Portunus puber* and almost the same size and colour. Rostrum bent at a rather more acute angle. Eight setæ to last pleopods, sometimes seven. It is very difficult to distinguish this megalopa from *P. pusillus*, indeed almost impossible, until the crab is obtained from it, which is always distinguishable by the front of the carapace, which is hairy with only very faint lobes.

First Young Crab Stage 1·6 mm. across carapace. Front very slightly three-lobed, hairy. Lateral teeth as in *P. puber* and narrow paddles to last legs. Later young stages were obtained from the first up to the fifth young stage, measuring respectively across the carapace:—1·6, 2·5, 3·2, 4·2, 5·1, 6·2 mm. As in *P. puber*, the carapace broadens rapidly, and by the fifth stage the crab is very like the adult, the front being flat and hairy. The following dates show the times taken for the young crabs to change:—

First young crab from megalopa ...	2.7.26
Second young crab from first.........	10.7.26
Third young crab from second	20.7.26
Fourth young crab from third	29.7.26
Fifth young crab from fourth	9.8.26
Sixth young crab from fifth	23.8.26

As in *P. puber*, the later moults take longer.

PORTUNUS PUSILLUS Leach. (Pl. I. fig. 4; Pl. IV. fig. 5; Pl. VII. fig. 1.)

The "Dwarf Swimming Crab" is common both inside and outside the Sound on sandy bottoms. Berried females from February to August, chiefly spring and early summer. Zoeæ and megalopæ very common in the plankton in spring and summer. Eggs hatched in aquaria as pre-zoeæ, which soon changed to first zoeæ. One first zoea feeding on *Echinus* larvæ changed to the second zoea, but no further stages were reared. Later stages from the plankton changed to megalopæ and then to young crabs. Cano (1893) gives a good figure of the first zoea, which is copied by Williamson (1915). Otherwise the life-history has not been described.

Eggs orange-red. Early eggs 0·28 mm., late eggs 0·32 mm. across.

Pre-zoea about 1·28 mm. long, soon changing to the first zoea.

First zoea about 1·3 mm. long. From spine to spine about the same. Colour very like *P. arcuatus*, but with a diffuse very pale pinkish tinge among the yellow. Telson and spines of carapace colourless. Both spines curved. All zoeal stages very common in the plankton, but easily confused with other species, especially *P. arcuatus*. Edge of carapace finely denticulated, changing to long hairs in later stages. Last zoea still retaining the pinkish tinge, about 3·3 mm. long, from spine to spine 2·5 mm., the spines, especially the rostral, thus greatly reduced in proportion to the body-length. Dorsal spine colourless or with a very pale yellow tinge. Telson with three lateral teeth in all stages, an extra pair of internal setæ in the third or fourth stage, and two extra pairs in the fourth and fifth. *Megalopa* from last zoea from plankton, very like *P. puber* and *P. arcuatus*, especially the latter, as it has seven spines on the last pleopods, sometimes eight. Rostrum bent at an angle like *P. arcuatus*, size and colour almost the same. The megalopa changed to the young crab, and several later stages obtained from this.

First Young Crab Stage with three well-developed lobes in front, lateral teeth as in *P. puber* and *P. arcuatus*, and narrow paddles to last legs. Carapace 2 mm. across, nearly circular. Later stages measure 2·5, 3·5 (one missed as the skin was eaten), and 7 mm. The following dates show the times taken for one crab to change its skin:—

Megalopa to first young crab	1.7.26
Second young crab from first	10.7.26
Third young crab from second	18.7.26
Fourth young crab from third	20.7.26
Fifth young crab from fourth.........	26.7.26

The young crab can be recognized as *P. pusillus* from the first stage, the front lobes being prominent compared with *P. puber* and *P. arcuatus*, which are the only species that can be confused with it (*P. corrugatus* not being known). All three have the second and fourth lateral teeth of carapace very small, the normal shape having been reached by about the fifth stage.

PORTUNUS MARMOREUS Leach. (Pl. I. fig. 5; Pl. VI. fig. 3.)

The "Marbled Swimming Crab" is fairly common both inside and outside the Sound on sandy bottoms. It is quite distinct from *P. holsatus*, as Palmer (*op. cit.*) has shown, although some workers were inclined to place it in the same species. The zoeæ are quite different in colouring and the megalopæ distinct. Both zoeæ and megalopæ occur frequently in the plankton in spring and summer, but are difficult to identify, as the older zoeæ are very like the other species and the megalopa very like that of *P. puber* and *P. holsatus*. Berried crabs occur occasionally in spring and summer. The eggs were hatched out in the aquarium as pre-zoeæ which changed to first zoeæ. One second zoea only was obtained from these, and this did not live. Later zoeæ were collected from the plankton and kept until the megalopæ and crabs emerged from them. Thompson (1835) hatched out the zoea, but the figure given might belong to any crab with lateral spines on the carapace, and the three laterals on the telson are not shown. He also figures a megalopa which possibly may belong to this species. Except for these no work has been done on the larvæ of *P. marmoreus*.

Eggs orange-red, changing to brownish. Early eggs 0·28 mm., late eggs 0·35 mm. across.

Pre-zoea about 1·12 mm. long, soon changing to the first zoea.

First zoea about 1·4 mm. long. From spine to spine about the same. Both spines curved. Colour yellowish-orange and pink. Telson pink. Eye blackish-blue, with yellow spreading dorsally outside it. Slight yellow spot or streak on dorsal spine turning to pink, usually accompanied by black. Black along intestine, mouth-parts, under lateral spines of carapace, and ventrally along abdomen. Edge of carapace smooth in first zoea, armed with long hairs in later stages. Later stages from plankton much like *P. depurator*, but smaller and distinguished by pinkish dorsal spine and telson. Length of fourth zoea about 2·9 mm., from spine to spine about the same. Last zoea changed to megalopa, and this to young crab. The later zoeæ agree with *P. depurator*, *arcuatus*, and *pusillus* in having three lateral spines on telson in all stages. In size they come between *P. depurator* and *P. arcuatus* and *pusillus*.

Megalopa much like that of *P. puber*, but may be larger, the size varying. Rostrum bent at a rather more acute angle. Ten setæ on last pleopods. The megalopa changed to the first young crab stage.

First Young Crab Stage differs from the three foregoing species in having the second and fourth lateral teeth of carapace more pronounced and in having broader paddles on the last legs. Carapace 2·4 mm. across. The young stages are all very much like *P. holsatus*, but can be distinguished on close examination.

PORTUNUS HOLSATUS Fabr. (Pl. I. fig. 6; Pl. VI. fig. 2.)

The "Livid Swimming Crab" is much like *P. marmoreus*, but quite a distinct species. It occurs more frequently than *P. marmoreus*, but in the same situations both inside and outside the Sound. Zoeæ and megalopæ common in the plankton in spring and summer and also berried crabs. The eggs were hatched out in aquaria and pre-zoeæ and first zoeæ obtained. Only one second zoea came through, and that did not live. Later zoeæ from the plankton changed to megalopæ, and these and also megalopæ from the plankton changed to young crabs. The later zoeæ were not distinguished from the other *Portunus* species in the plankton. Williamson (1911, 1915) hatched the pre-zoea, and describes the first, third, fourth, and fifth zoeæ, also the megalopa of *P. holsatus*, and figures most of them. No other work has been done on this species.

Eggs orange-red, changing to brownish. Early eggs 0·25 mm., late eggs 0·32 mm. across.

Pre-zoea about 1 mm. long or rather longer, quickly changing to the first zoea.

First zoea about 1·3 mm. long. From spine to spine about the same. Spines curved. Colour brownish merging into brownish-pink. Dorsal spine with black chromatophore. Eyes blackish-blue with a yellow glint, black chromatophores among the brown, especially in the region of the intestine and ventrally on the abdomen. Yellow at the sides of carapace. There may be a little pigment in the dorsal spine, especially in the later stages. The last zoea changed to the megalopa.

Megalopa, one of the largest of the *Portunus* species. Like *P. marmoreus*, but larger and usually lighter coloured. Carapace 1·76 to 2·25 mm. in length, not including the bent rostrum. Rostrum bent at about the same angle as *P. marmoreus*. Last pleopods with ten setæ, changed into a very large crab, but smaller crabs of this species have been obtained from other megalopæ from the plankton.

First Young Crab Stage 3·2 mm. across the carapace. Paddles on last legs broad. Later stages measured respectively across carapace 6, 10, 15, 20, 25 mm.

The following dates show times of changing skin in one crab:—

First young crab from megalopa......	14.6.26
Second young crab from first	23.6.26
Third young crab from second	1.7.26
Fourth young crab from third	13.7.26
Fifth young crab from fourth.	3.8.26

The young crab is very like *P. marmoreus*, with the second and fourth teeth of the carapace, although smaller than the other at first, still much larger than they are in *P. puber*, *arcuatus*, and *pusillus*, and the three teeth in front are very distinct. It is surprising that *P. holsatus* grows so much more quickly than any of the others, reaching a breadth of carapace of 25 mm. in less than two months, a larger growth than in any other crab reared.

PORTUNUS DEPURATOR (L.) (Pl. I. fig. 7; Pl. VI. fig. 1.)

The "Cleanser Swimming Crab" is the commonest of all the *Portunus* species in the district, occurring abundantly both inside and outside the Sound. Berried crabs in spring, summer, and autumn, rarely in winter, chiefly in spring; zoeæ and megalopæ in the plankton most of the year, especially in spring and early summer. The eggs were hatched out in the aquarium and pre-zoeæ and first zoeæ obtained, but only one or two came through to the second, third, and fourth zoea, and did not live. Later stages from the plankton changed into megalopæ, and these into young crabs. This is perhaps the best known of the *Portunus* species in the larval stages. Claus (1876) gives a drawing of the megalopa, Thompson (1835 *a*) and Couch (1843) hatched out the first zoea, and Björk (1913) gives a good account of it from the plankton, describing the first, third, fourth, and fifth zoeæ, megalopa, and first young stage with figures. Williamson (1911–1915) also describes certain stages.

Eggs light brown, changing to a darker speckled brown. Early eggs 0·32 mm., late eggs 0·4 mm. across.

Pre-zoea about 1·12 mm. long, living a few hours and then changing to the first zoea.

First zoea about 1·6 mm. long. From spine to spine about the same. Spines curved. Colour black and yellow. Black chromotophores on front of dorsal spine, mouth-parts, region of intestine, and ventrally along abdomen; yellow accompanying the black. Eyes bluish black with a yellow glint. In later zoeæ the dorsal spine becomes dusky, with black and yellow spreading up it, sometimes yellow, owing to the contraction of the chromotophores.

Zoeal stages much like the other species, but can be recognized by their colour. Edge of carapace smooth in first zoea, edged with long hairs in the others. All three lateral spines of telson present in all stages. One pair of extra internal setæ arising in second zoea or later, two pairs in fourth or fifth stage. Last zoea about 4 mm. long. From spine to spine about 3·5 mm.

Megalopa differs from all the other *Portunus* species in having the rostrum sticking straight out and not bent. Length of carapace (including rostrum) 2 mm. Last pleopods with ten setæ, very rarely nine.

First Young Crab Stage very like *P. holsatus* and *P. marmoreus*. The three teeth very distinct in front and the second and fourth teeth more distinct than in *puber*, *arcuatus*, and *pusillus*. The very young stages are distinguished with difficulty from *holsatus* and *marmoreus*, but at about the third or fourth stage the characteristic rugosities appear on the carapace. By carefully comparing the little crabs with Palmer's diagnosis (*op. cit.*) the three species can be distinguished, however, even at the first stage. First stage 3·8 mm. across the carapace, successive moultings 5·2, 7, and 9 2 mm. The following dates show the times taken to moult:—

First young crab from megalopa	...	15.6.26
Second young crab from first	....	23.6.26
Third young crab from second	......	9.7.26
Fourth young crab from third	......	18.7.26
Fifth young crab from fourth	......	26.7.26

The zoeæ differ little except in colour, all the species being much alike in structure. The megalopæ fall into two groups, those with ten setæ on the last pleopods and those with seven or eight. From those with ten setæ *P. depurator* is separated at once by its straight rostrum, leaving *P. puber*, *P. marmoreus*, and *P. holsatus*, the last being bigger than the other two. *P. puber* and *P. marmoreus* are so much alike that they can hardly be told apart, *P. arcuatus* and *P. pusillus*, with seven or eight setæ, also hardly differing at all from one another. To be quite sure about these difficult cases the only safe way is to rear them to the crab stages. The young crabs fall into two groups—those with narrow paddles and very indistinct second and fourth lateral teeth (*P. puber*, *P. arcuatus*, and *P. pusillus*), all of which can be distinguished from one another by the front of the carapace, and those with broad paddles, the second and fourth lateral teeth not being so rudimentary, although distinctly smaller than the other in the early stages (*P. marmoreus*, *P. holsatus*, and *P. depurator*).

Genus BATHYNECTES.

BATHYNECTES LONGIPES Risso. (Pl. IV. fig. 7.)

The "Long-Legged Swimming Crab" is very like a *Portunus*, and occurs rarely on the dredging grounds outside the Sound.

One berried female was taken in July 1926 and the pre-zoea and first zoea obtained. Unfortunately these did not live. No larvæ were found in the plankton. No previous work has been done on these larvæ, which resemble those of *Portunus* very closely, and no special characters separate the early stage from this genus.

Eggs light brownish when ready to hatch. Measurements not taken.

Pre-zoea about 1·25 mm. long, quickly changing to the first zoea. Agreeing in structure with *Portunus*.

First zoea about 1·25 mm. long. From spine to spine about the same. Spines curved. Lateral spines rather long, about half the length of the rostral spines. Structure of body like *Portunus*. Colour brownish with a little yellow. Eye bluish-black, flecked with yellow. Darkish brown in mouth-region and alimentary canal and ventrally on abdomen, mixed with black and yellow. Drawing in colour not made.

Genus POLYBIUS.

POLYBIUS HENSLOWI Leach. (Pl. IV. fig. 6.)

"Henslow's Swimming Crab" is rare in the district, and females are seldom found. One occurred in July 1927 from the Rame mud outside the Sound, but was not in berry. In September 1898, Mr. R. A. Todd found a berried female and hatched out the zoeæ. Apparently the pre-zoeæ were not seen. He has kindly given me the zoeæ. No colour notes are available. No zoeæ have been observed in the plankton, and later stages are not known. Couch (1843) hatched out the zoeæ, but does not describe them. No further work has been done on them.

First zoea resembles *Portunus* and *Bathynectes* very closely, and no characters could be found which separate them. About 1 mm. long. From spine to spine about the same. Spines much curved. Lateral spines fairly long.

Subfamily *CARCININÆ*.

Four zoeal stages. No lateral spines on carapace. Telson with three lateral spines in the early stages, dwindling to one in the later stages. No extra internal spines. No lateral spines on abdominal segments in any stage. Megalopa with rostral spine sticking out horizontally; protuberances on carapace not conspicuous. Only rudiments of spines on coxæ of legs 2 to 5. First young stage without paddles on last legs, although these bear long hairs.

Genus CARCINUS.

With the characters of the subfamily.

CARCINUS MÆNAS Penn. (Text-fig. 2, 7 to 10 & Pl. I. fig. 8; Pl. VII. figs. 3–5.)

The "Common Shore-Crab" is the commonest and best known of all British crabs. It occurs along the coast everywhere, and is in berry all the year round, although it chiefly breeds in spring and summer. Larvæ abundant in the plankton, especially in spring and early summer. Very young crab stages, from about the second stage, may be found along the coast, particularly in the estuaries. Much work has been done on this species, and its life-history is well known. The young were hatched in the laboratory and reared to the fourth (last) zoea, later zoeæ being taken from the plankton and reared to crabs.

Thompson (1835) was the first to hatch out and describe the zoea, which he figures. Du Cane (1839) describes and figures the pre-zoea and zoea. Goodwin (1842) and Couch (1843) both described the larvæ, Couch figuring the zoea, megalopa, and two young stages. Spence-Bate (1858) in his elaborate monograph describes the life-history. This is not entirely correct, although containing much valuable observation. Unfortunately one of his figures of the megalopa (E, pl. xlii.), which really belongs to a different species, probably *Cancer*, has crept into some well-known text-books (Korscheldt and Heider 1890, Calman 1909). Spence-Bate thought there were several megalopal stages, when really there is only one. His mistake is easily accounted for when it is realized that he picked the various stages out of the plankton. Faxon (1800) gives a very fine figure of the pre-zoea and zoea, and Brook (1884) gives excellent drawings of the megalopa and young stages, omitting, however, the feelers on the last legs of the megalopa. Cano (1892 *b*) figures zoeæ and megalopa, but gives the latter a dorsal spine. He suggests that Slabber's (1778) *Monoculus taurus* belongs to this species. Williamson (1900, 1902 1915) describes the whole life-history. He hatched out the first zoea, which moulted to the second, the later stages being collected from the plankton and kept until they changed. He figures most of the stages or parts of them, describing all essentials accurately. Miss Jorgensen reared *Carcinus* from the egg to megalopa in an aërated aquarium at Cullercoats. It is thus seen that *Carcinus mænas* is a much-described crab, and very little need be said about it here.

Eggs yellowish-brown, changing to almost black. Early eggs 0·32 mm. Late eggs 0·4 mm. across.

Pre-zoea about 1·28 mm. long, living for several hours before changing to the first zoea.

First zoea about 1·36 mm. long. From spine to spine about the same. Colour greenish-brown with yellow. Eye blackish, diffused with yellow. Many dark chromatophores, the most characteristic being a long and much-branched one along the side of the carapace which persists in the megalopa.

Second zoea about 1·76 mm. long. *Third zoea* about 2·56 mm. *Fourth zoea* about 3·2 mm.

Megalopa with a finely-pointed rostrum sticking out, but slightly bent. Length of carapace about 1·5 mm., including rostral spine. Inconspicuous protuberances on carapace. Five setæ on last pleopods.

First Young Crab Stage speckled brownish, with a little yellow and red. About 1·6 mm. across carapace. Front waved so that three lobes are faintly perceptible; armed with fine hairs. Second and fourth lateral teeth smaller than the others. Later stages measure 1·9, 2·8, 4·2, 6 (one broken), and 8 mm.; the tenth young stage died, measuring 22 mm. across. Carapace at first almost circular, gradually increasing in breadth, and at about the fifth stage looking something like the adult, although even in the first stage it is recognizable, being distinguished from *Portunus* by the last legs, which have no paddles. The following dates show the times taken for one crab to change into its successive stages:—

First young crab from megalopa ...	9.7.26
Second young crab from first	13.7.26
Third young crab from second	16.7.26
Fourth young crab from third	24.8.26

Subfamily *PORTUMNINÆ*.

Zoea not known. Megalopa like *Portunus*, except that there are no spines on the coxæ of the second to the fourth legs; the hook on the ischia of the first very large. Young crab with the last legs adapted for swimming, but with long hairs on one side only of the paddles.

Genus PORTUMNUS.

PORTUMNUS BIGUTTATUS (Risso). (Pl. VIII. figs. 1–3.)

This is a very rare crab in the Plymouth district, being dredged only occasionally. The only larva known is a megalopa collected by Mr. Robert Gurney in August 1902. This he states was an intense blue. He kept it until it changed into the young crab, and kindly sent me both specimens.

Megalopa large and heavily built. Rostrum sticks out horizontally in a long spine. Protuberances on carapace apparently not prominent (as only the cast skin was available, this may not be correct). Abdomen broad. Last pleopods with eleven setæ. Length of carapace 2·2 mm.

First Young Crab Stage 1·9 mm. across carapace; length of carapace 2·3 mm. Three indistinct rounded lobes in front, five flat teeth laterally, the second and fourth the smallest. Last joint of last leg adapted for swimming, but with long hairs only on one side as in the adult.

Family PIRIMELIDÆ (?), fam. n.

(This family is placed here with a query, as the identity of the larva on which it is based is not quite certain.) Last zoea with two lateral spines on telson, one pair extra internal setæ. Hook-like knobs on second abdominal segment only. No long lateral spines. Megalopa with pointed rostrum sticking straight out and a hook-like dorsal spine just behind the centre of the carapace. Large hook on ischia of first leg. No hook-like spines on other legs. First and second young crab stages with three rostral and five lateral teeth to carapace, all sharp and prominent; last legs with swimming-paddles, penultimate legs with long hairs.

Genus Pirimela (?).

Almost certainly four zoeal stages (only last known). No lateral spines on carapace. No lateral spines on third to fifth abdominal segments. Dorsal and rostral spines long, especially dorsal.

Pirimela denticulata (?). (Pl. I. fig. 9; Pl. VII. fig. 6; Pl. VIII. figs. 4-6.)

Apparently closely related to *Carcinus* and also to *Portunus* and *Portumnus* is a crab found in the Plymouth plankton in the last zoea and megalopa. The zoea was kept until it had changed into a megalopa, and the megalopa changed to a crab. One first young crab changed into a second and then died. We have, therefore, only these four stages at present. The larvæ are rare, occurring only in the late summer or early autumn, and only a few specimens were obtained. They are exceptionally interesting, and seem to link the Portunidæ with the Canceridæ in an even more definite way than *Carcinus*. The only crab which it is at all likely to be is *Pirimela denticulata* Montagu, one of the rare crabs of the district occurring occasionally at extreme low water among rocks, under stones, and in gravel; and it is here suggested that it belongs to that species. It is difficult to imagine what else it could be, as we know something about all the other larvæ of the Plymouth Brachyrhyncha, and not one can be identified with these specimens. The genus *Pirimela* is usually placed in the Canceridæ with a separate subgenus, the *Pirimelinæ*. It is recorded as breeding in this district in March and April. Kinahan (1856-59) hatched out the zoea, and describes and figures it as having lateral spines on the carapace and resembling *Cancer pagurus* closely. This is one point against the present identification, as the zoea has no lateral spines. The only other writer who refers to the larva is Cano (1891), who figures a megalopa having a pointed rostrum and no dorsal spine: but a figure of the first leg is shown with a large hook on the ischia, very similar to our specimens. The rostrum is like our megalopa, also the first leg, but our megalopa has a dorsal spine. This is, however, near the centre of the carapace, and does not stick out behind. It might easily have been overlooked by Cano. He also figures a second megalopa and a first young crab stage which he attributes to *Pirimela*. This last is not at all like our specimens. A point against its belonging to the Cancridæ is the fact that the young crab has distinct swimming-paddles on its last legs, the penultimate legs also bearing long hairs. The legs, however, become more normal in the second stage, although the last legs still have distinct paddles and the little crab can swim beautifully.

The following is a brief description :—

Last zoea (evidently the fourth) with no lateral spines to carapace. Length from dorsal spine to rostral spine exceeding the body-length; body-length 3·2 mm., from spine to spine 3·6 mm. Dorsal spine very long. Carapace edged with long hairs. Ten setæ on maxillipedes. Hook-like knobs on second abdominal segment only. No lateral spines on segments 3 to 5. Telson with one lateral spine and no extra internal setæ. Colour chiefly brown and orange-pink, with a long-branched brown chromatophore, accompanied by orange on the side of the carapace in the same position and of the same shape as in *Carcinus*. Other brown chromatophores on carapace and ventrally along abdomen accompanied by orange-pink, which also occurs on the dorsal spine. Antennæ like all the Portunidæ and Cancridæ. Antennule slightly jointed. Rudimentary legs well developed.

Megalopa with the same colouring; the long lateral chromatophore still very conspicuous as in *Carcinus*. Rostrum pointed, sticking straight out horizontally. A short hook-shaped spine, broad at the base, sticking up just behind the centre of the carapace. Carapace broad, with inconspicuous protuberances; length 2 mm. (including rostral spine), breadth 1·28 mm. Seven spines to last pleopods. Large hook on ischia of first leg, none on other legs.

First Young Crab Stage. Length of carapace 2·4 mm., breadth about the same. Three very sharply indented and rounded teeth in front, five sharp and fairly long teeth laterally. Much the shape of *Portumnus*. Very light-coloured—yellowish-brown with two dark spots dorsally behind the eyes. The two last pair of legs adapted for swimming, with long hairs on both sides, the last joint of the last leg paddle-shaped.

Second Young Crab Stage. Length of carapace 3·52 mm., breadth 3·68 mm. Much like the first stage. Penultimate legs more normal, but still with long hairs; last legs still with paddles. The specimen is apparently a male with a long and narrow abdomen, the third and fourth segments showing a suture, but not divided so distinctly as the other joints.

From this description we apparently have a close relation of the Portunidæ (having three teeth in front and five laterally in the young crab), resembling *Portunus*, *Carcinus*, and *Portumnus*, but differing from all in important ways. It agrees with *Portunus* in the swimming-legs of the young crab, and with *Carcinus* in the arrangement of its chromatophores, in having four zoeal stages and in the absence of lateral spines on the carapace, in having no lateral spines on segments 2 to 5 and only one lateral spine on the telson and no extra internal spines in the last zoea. In the megalopa it resembles *Carcinus* in colouring and the form of the rostrum, differing in having a dorsal spine on the carapace and no trace of hooks on the coxæ of the second to the fourth legs, resembling *Portumnus* in this and the large hook on the ischia of the first leg. In the young crab stages it resembles *Portumnus* in shape, but differs in having long hairs on both sides of the swimming-paddles.

How can we reconcile these characters with *Pirimela denticulata*? In the first place, in the young crab the front of the carapace and the lateral teeth strongly suggest that species, the front teeth being long and narrow, the laterals very sharp. The carapace is, of course, much longer compared with the width than in the adult; but this is so in all young crabs except in those which keep that shape in the adult (*Portumnus, Thia, Corystes*). The abdomen also suggests it, as it is very long and narrow and unlike *Portunus*. A comparison with a half-grown *Pirimela* shows a somewhat similar shape. The megalopa has a dorsal spine, which is characteristic of *Cancer. Atelecyclus*, and *Corystes*, but not of the Portunidæ. Finally, all the Plymouth Portunidæ are known in at least one zoeal stage except *Portumnus*, which we know in the megalopa and young stages and which are certainly not identical with the present species. The only other British *Portunus* is *P. tuberculatus*, which has not been as yet found at Plymouth; but the specimens here described cannot, I think, by any possibility belong to a true *Portunus*. *Pirimela* is the only species of any of the Brachyrhyncha occurring at Plymouth that I have not personally seen in the zoeal stage. There seem to be good reasons for regarding this as *Pirimela*; but if this be correct, it is most interesting to find that it goes through a swimming stage, although the last legs in the adult have a distinct fringe of long hairs on one side. I should suggest that, as it seems to have distinct affinities with the Cancridæ in the adult and even in the megalopa, but also shows relationship in the young stages with the Portunidæ, especially with *Carcinus*, it be placed by itself in a family, the Pirimelidæ, having a position between the Portunidæ and the Cancridæ, and that *Carcinus* be regarded as its nearest relative, *Portunus* and *Portumnus* being also closely connected. Is it not possible that a primitive form may have been free-swimming, and that *Carcinus* is more highly evolved than *Portunus*?

Family CANCRIDÆ.

Pre-zoea with four long spines over exopodite of antenna. Five zoeal stages. Carapace with dorsal, rostral, and lateral spines. Antenna as in the Portunidæ. Hook-like knobs on second abdominal segment only in all stages. One and two extra

internal setæ in later stages. Megalopa with pointed rostrum sticking out horizontally; dorsal spine on carapace sticking out horizontally behind. Spine on coxæ of second leg. Hook on ischia of first leg present or absent. First young stage without swimming-legs. Carapace round, with three denticulated teeth in front and five laterally with rudimentary teeth in between. Later young stages changing according to genus.

Subfamily *CANCRINÆ.*

Genus CANCER.

Zoeæ with the characters of the family. Megalopa with large hook on ischia of first leg, small hook on second. The American species, *Cancer amœnus*, worked out by Conolly (1923), agrees with our species in nearly every important particular except for the fact that he describes four zoeal stages only, the last having eleven and twelve setæ on the maxillipedes. The true fourth zoea must either be "jumped" or was present but not found, the specimen being taken from the plankton. It seems likely that the latter explanation is the correct one.

CANCER PAGURUS L. (Text-fig. 2, 11 to 15 & Pl. I. fig. 10; Pl. V. fig. 5; Pl. X. figs. 3–5.)

The "Edible Crab" is common in the district, berried crabs occurring in spring and summer, chiefly in the spring, and zoeæ and megalopæ in spring and early summer are abundant in the plankton. Young crabs from the first stage onwards can be found among the rocks under stones at low tide. The female carries her eggs for many months. It is a remarkable fact that this well-known crab should still be so little known in its larval stages. When these crab studies were begun in 1926, no reference could be found to any zoeal stages later than the second, and the megalopa had never been described except by Couch, who was the first to see it but gave no details. Eggs were hatched out in the laboratory, and pre-zoea and first zoea obtained, but they were extremely difficult to rear, only one specimen reaching the third zoeal stage. Later zoeæ were collected from the plankton which changed to megalopæ, and these to crabs.

Cancer was first hatched by Thompson (1829), later by Couch (1843), who figures it but omits the lateral spine. Couch (1853) also discovered the megalopa in a bowl in which he had left some zoeæ hatched from the eggs, so was really the first and only worker to rear this crab. Williamson (1900, 1903, 1911, 1915) describes and figures the pre-zoea and first zoea, giving also an account of the growth of young crabs. Pearson (1908) figures the zoea. Cunningham (1898) in a most interesting paper describes the very young *Cancer* (evidently the first crab stage), showing how closely related it is to *Atelecyclus*. The whole of the life-history is now available.

Eggs a brilliant orange, changing to a brownish colour. Early eggs 0·32 mm., late eggs 0·4 mm. across.

Pre-zoea about 1·76 mm. in length, and remains moving about in the water for some hours before changing into the first zoea.

First zoea about 1·76 mm. long. From spine to spine 2·4 mm. Colour chiefly orange and red, merging into pale yellow over the carapace and dorsally. Dorsal spine bright red with a little black in the centre of the front, rostral spine pale pink. Eye blackish, with yellow and orange. Telson red with pink tips, red on carapace and sides of abdomen. Black chromatophores in mouth-region, lateral part of carapace, base of lateral spines, and ventrally along abdomen; a streak or two along intestine. Dorsal and rostral spines nearly straight, laterals short in all stages. Antennal exopodite about one-third the length of the spinous process in all stages.

Second zoea about 2·24 mm. long. From spine to spine 3·2 mm. Very like first zoea, but with rudimentary limbs slightly more developed.

Third zoea about 2·5 mm. long. From spine to spine about 3·36 mm. Pleopods and antennal flagellum beginning. Six abdominal segments plus telson. Lateral spines beginning on third to fifth segments. Rudimentary legs more developed. One pair of extra internal setæ on telson. Long hairs on edge of carapace and in all the succeeding zoeæ.

Fourth zoea about 3 mm. long. From spine to spine 4·4 mm. Pleopods and antennal flagellum longer. Lateral spines longer on abdominal segments. Two pairs of extra internal spines to telson. Rudimentary limbs more developed.

Fifth zoea about 4 mm. long. From spine to spine 4·5 mm. Pleopods long. Lateral spines on abdominal segments long. Rudimentary limbs well developed and showing traces of joints. First leg chelate. Antennules jointed with branch. Antennal flagellum slightly jointed. Mandible with palp.

Megalopa with pointed rostrum. Dorsal spine sticking out behind carapace almost horizontally, but slightly curled upwards. Colour orange and red with very little black. Rostral spine yellow, dorsal red. Length of carapace (including rostral spine) 2·24 mm. Eight spines on last pleopods, rarely nine. Large hook on ischia of first leg, small hook on second. Prominences on carapace indistinct.

First Young Crab Stage nearly round, with three denticulated lobes in front and five denticulated lateral teeth with rudimentary teeth in between. Colour orange. Length of carapace 2·4 mm., breadth about the same. This is the stage figured by Cunningham (*op. cit.*), which is so like *Atelecyclus*. The little crab covers its body with anything it can find, the second and third young stages doing the same.

Second Young Crab Stage with the lobes not nearly so spiny, but the margins crenulated. Ten teeth laterally. Length of carapace 2·64 mm., breadth 3 mm. The breadth now gradually increases and the adult shape is soon assumed. Breadth of carapace in third to sixth young stages 5·28, 6·7, 10, and 14 mm. The following dates show the times of changing skin in one crab:—

First young crab from megalopa ...	7. 7.26
Second young crab from first	19. 7.26
Third young crab from second	13. 8·26
Fourth young crab from third	31. 8.26
Fifth young crab from fourth	27. 9.26
Sixth young crab from fifth	30.11.26

Subfamily *ATELECYCLINÆ*.

Genus ATELECYCLUS.

Like *Cancer* in the zoeal stages. Megalopa without a large hook on the ischia of the first leg, but a small hook on the ischia of the second.

ATELECYCLUS SEPTEMDENTATUS Leach. (Pl. II. fig. 1; Pl. IX. figs. 1–6; Pl. X. figs. 1–2.)

The "Circular Crab" occurs commonly in the district both inside and outside the Sound on the usual dredging and trawling grounds. Berried females abundant in early spring. Larvæ common in the plankton in spring, rare in summer, and absent altogether in autumn and winter. The pre-zoeæ and first zoeæ were hatched from the eggs, but only one second zoea appeared, and this died. Later stages were collected from the plankton, and kept until they changed into megalopæ and crabs. Nothing is known up to the present time of any of the larval stages of this crab, which are so like *Cancer* and are evidently very closely related to it. Cunningham (*op. cit.*) knew the very early young crab stages, and compares them with *Cancer*, showing how like they are to similar stages of that species.

Eggs orange, turning to light brown. Early eggs 3·5 mm., later eggs 4·2 mm. across.

Pre-zoea about 1·36 mm. long, living for some hours before setting free the first zoea.

First zoea about 1·6 mm. long. From spine to spine about the same. Antennal exopodite about half the length of the spinous process, gradually lengthening in the later stages. Colour orange and yellow with very little red; black chromatophores accompanied by brownish-orange conspicuous on carapace and ventrally on abdomen. Dorsal spine colourless, turning to pale yellow, never red. Dorsal and rostral spines curved, becoming straighter in the later stages. All the zoeal stages agree so much in essential characters with *Cancer* that it is not necessary to describe them in detail.

Second zoea about 2·24 mm. From spine to spine about the same.

Third zoea about 3 mm. long. From spine to spine about the same.

Fourth zoea about 3·8 mm. long. From spine to spine about the same.

Fifth zoea about 4·2 mm. long. From spine to spine about the same.

Megalopa much the same shape as in *Cancer*, but larger; the dorsal spine shorter. Orange and yellow. Last pleopods with ten or eleven setæ. Carapace 2·7 mm. long, 1·6 mm. broad.

First Young Crab Stage very like the same stage in *Cancer*. Breadth of carapace of second young stage 2 mm. The second and later stages remain round, and can be easily distinguished from similar stages of *Cancer*. Both species are yellowish and orange, the colour deepening as the crab gets older. Both cover their bodies with extraneous material in the very early crab stages.

It has already been stated that the later zoeæ of *Portunus puber* resemble very closely those of *Cancer* and *Atelecyclus*. In the living specimens it is easy to distinguish them by their colour, *P. puber* being much more of an eosin-pink wiih a good deal of black, especially along the intestine, *Cancer* bright red and orange with only a little black, and *Atelecyclus* yellow and orange with very distinct and separate dark chromatophores, particularly on the carapace. In preserved material none of the colours can be relied on. *Atelecyclus* can be separated from the other two by its dorsal and rostral spines, which are shorter, but *Cancer* and *Portunus puber* resemble one another very closely in the last two stages. In *P. puber* the rostral spine is shorter than in *Cancer*, and in the earlier stages the dorsal also, but in the later stages the dorsal spines may be of the same length and straighter in *P. puber*. On the whole the best character is the length of the antennal exopodite compared with the length of the spinous process, which is also the best way of distinguishing *Cancer* from *Atelecyclus*. In *Portunus puber* the antennal exopodite is about one-half the length of the spinous process, in *Cancer* about one-third the length, and in the later stages of *Atelecyclus* more than half the length.

Family CORYSTIDÆ.

Antennal flagellum very long in later zoeæ. One lateral spine on telson in all stages. One to four pairs of extra internal setæ in later stages. Hook-like knobs on second abdominal segment only. Megalopa with three-toothed rostrum, lateral spines at edge of carapace, and a small dorsal spine behind the centre. First young stage with excavated rostrum forming two short horns.

Genus CORYSTES.

Five zoeal stages. All spines present on carapace. Antenna like *Portunus*, but with the flagellum growing fast and in the later stages exceeding the length of the spinous process. Lateral spines on abdominal segments 3 to 5 in later stages. Megalopa with three lateral spines at edge of carapace. Ischia of first leg with small hook; small hooks on coxæ of ischia of second to fourth legs. From the megalopa onwards the flagella which form the breathing-tube attain to the enormous length characteristic of this burrowing crab.

CORYSTES CASSIVELAUNUS (Pennant). (Pl. II. fig. 2; Pl. XIII. figs. 2–3.)

The "Masked Crab" is common on the dredging and trawling grounds both inside and outside the Sound. The berried females are usually rare, but occasionally occur in numbers. Six were once taken together in Cawsand Bay in April 1926, and the day after 72 were taken outside the Sound. In 1925 the only berried females taken in the year were two specimens in July. Unfortunately none of the eggs hatched, although the crabs carried them for months and lived for a long time. It was therefore necessary to collect the larval stages from the plankton and rear them to the crab stages in the laboratory. The zoeæ are very abundant in the plankton in spring and early summer, sometimes occurring in swarms, sometimes also the megalopæ. All of them are easily recognizable, as they are the largest crab larvæ, the very long dorsal and rostral spines in all stages except the last, and the length of the flagellum in the later stages, separating them from any of the others. All the five zoeal stages were obtained from the plankton and the megalopa, the earlier changing into the later stages, and the fifth into the megalopa in the laboratory. Young crabs up to the fifth stage were obtained from these megalopæ. The life-history from plankton specimens has been beautifully worked out by Gurney (1903), who gives very good illustrations. He, however, only recognized four zoeal stages, one, the third, being overlooked. In his drawing of the megalopa he omits the feelers at the end of the last leg, which are truly present and are of importance, being a distinguishing character of the typical Brachyrhyncha.

Eggs bright orange-red. Early eggs 0·4 mm., late eggs 0·48 mm. across.

Pre-zoea not known.

First zoea about 2·4 mm. long. From spine to spine 4 mm. Colour reddish-brown; dorsal and rostral spines pink, with a little dark brown irregularly splashed over it. Main part of carapace pinkish-brown, with dark brown chromatophores mixed with black above and below the intestine and in the mouth-parts, red, brown, and black along the abdomen, black ventrally and on the base of the maxillipedes. Eyes blackish-brown with a little yellow. Four setæ on maxillipedes.

Second zoea about 3·4 mm. From spine to spine 5·5 mm. Six setæ on maxillipedes. One extra internal pair of setæ on telson. This second zoea is rather more advanced than most of the second zoeæ of the Brachyrhyncha, having the sixth abdominal segment separated from the telson and the extra pair of internal spines. Pleopods show as small protuberances, and the antennal flagellum is beginning to form. Gurney suggests that here there may be more than one stage, as he found differences in the specimens. This may indicate the third stage, which he does not describe, for, although he attributes six setæ to the maxillipedes of this zoea, the figure shows nine and ten.

Third zoea about 4·5 mm. long. From spine to spine 8 mm. Antennal flagellum fairly long. Ten setæ to maxillipedes, which is exceptional in a third zoea, the usual number being eight. Two pairs of extra internal setæ to telson (exceptionally two on one side and one on the other).

Fourth zoea about 5·5 mm. long. From spine to spine 9·5 mm. Antennal flagellum much longer. Twelve setæ to maxillipedes, usually plus one lateral seta. This, again, is exceptional in a fourth zoea, the usual number being ten. Three pairs of extra internal setæ to telson (or three on one side and two on the other), again unusual and more than the typical number. Legs already slightly jointed and pleopods fairly long.

Fifth zoea about 7·5 mm. long. From spine to spine 9·6 mm. Fourteen setæ to maxillipedes plus two small laterals. Four extra pairs of internal setæ to telson, more than in any other known crab. Legs jointed and much developed, the whole form heavy and length of spines much reduced compared with the body-length. Flagellum a good deal longer than the spinous process.

Megalopa very large and far advanced. Carapace 3·36 mm. long, 3·24 mm. broad. Length of antennal flagellum 3·5 mm. Small dorsal spine behind centre of carapace. A pair of spines behind the eyes. Three teeth at edge of carapace, three in front. Ten setæ on last pleopods. This megalopa, with its three-toothed rostrum and three lateral teeth on the carapace, is more like a crab stage than a megalopa, and resembles a young Portunid which has already been shown by Gurney, who mentions that it may already burrow in sand, although capable of swimming well with its pleopods. Altogether the different larval stages of *Corystes* are exceptionally advanced.

First Young Crab Stage with two-horned rostrum. Four lateral teeth to carapace, the fourth minute and near the hind end. Length of carapace 4·48 mm., breadth the same. As the crab grows, the carapace becomes longer.

The following data show the time taken in successive changes of skin in one crab (♂) from last zoea to fifth crab stage:—

First young crab from megalopa ...	20.5.26
Second young crab from first	31.5.26
Third young crab from second	14.6.26
Fourth young crab from third	22.7.26
Fifth young crab from fourth	11.8.26

Family THIIDÆ, fam. n.

Thia is usually placed with or near *Atelecyclus*. It is, however, different in many ways, and in its larval stages does not fit into any family, although apparently near the Canceridæ and Corystidæ. It is thought advisable to place it in a separate family.

One lateral spine to telson in all stages. One pair of extra internal setæ in stages 2 to 4. Hook-like knobs on second abdominal segment only. Megalopa with pointed rostrum slightly bent; smooth carapace without dorsal spine. First young crab stage with three lobes slightly indicated in front and four lateral teeth on carapace, and a fifth rudimentary tooth between the second and third.

Genus THIA.

Four zoeal stages. All spines present on carapace. Antenna like *Portunus*. No lateral spines on abdominal segments in later stages. Megalopa without spines on ischia of first leg and none on coxæ of legs 2 to 4, although there appears to be remnants in the shape of small knobs.

THIA POLITA Leach. (Pl. I. fig. 11; Pl. VIII. figs. 7–8.)

Very rare in this district and only occasionally dredged outside the Sound. It has not been seen here in berry, but the larvæ occur in the plankton in late summer. Three out of the four zoeal stages have been collected as well as the megalopa, the latter also being obtained from the last zoea and young crabs from these. Claus (1876) figures the first zoea, telson, and antenna, but shows two lateral spines on the telson, whilst I find only one. Cano (1892) has given a good account of the larvæ, describing three zoeæ, the megalopa, and the young crab. He omits the third zoea which occurs at Plymouth, the first not being seen. Pre-zoea not known. Zoeæ with very long dorsal spines, straight, the rostral a good deal shorter. Colour—much chocolate-brown occurring as a bar at about the middle of the dorsal spine, a strong line accompanying the front part of the intestine, along ventral surface of abdomen, on mandible, and at sides of carapace. Eye blackish-brown with yellow. Yellow accompanying brown on dorsal spine; sides of carapace and abdomen with reddish-orange. Telson slightly orange, turning to yellow.

First zoea described and figured by Cano and figured by Claus. Not seen at Plymouth.

Second zoea about 3·36 mm. long. From spine to spine 3·5 mm. Dorsal spine 1·8 mm., rostral 0·96 mm. long. Legs fairly well developed. Long hairs round edge of carapace.

Third zoea about 3·84 mm. long. From spine to spine 4·6 mm. Dorsal spine 2·24 mm., rostral 1·12 mm. long. Pleopods conspicuous.

Fourth zoea about 4·16 mm. long. From spine to spine 5·28 mm. Dorsal spine 2·56 mm., rostral 1·6 mm. long. Ten setæ on maxillipedes plus two small laterals. Legs jointed. Antennal flagellum jointed. Mandible with palp. Pleopods long.

Megalopa light-coloured, speckled, and smooth. Carapace (including rostral spine) 2·28 mm. long, 1·6 mm. broad. Eight setæ to last pleopods.

First Young Crab Stage whitish, porcellanous, faint yellowish in region of liver. Front faintly three-lobed, with centre protruding. Four lateral teeth, a fifth being indicated between second and third, disappearing in second young stage, and in this stage the front is no longer three-lobed, but slightly pointed. Breadth of carapace of first stage 2·8 mm. The first few stages readily cover themselves with extraneous matter like *Cancer*.

Family XANTHIDÆ.

Pre-zoea with four long spines over antennal exopodite. Zoeæ with three lateral spines on telson in all stages, or one tending to disappear in later stages (in certain foreign forms, apparently, there may be none at all). One or two extra pairs of internal setæ in later stages, or these may be absent. Antenna with rudimentary exopodite, or with one nearly as long as the spinous process. Lateral spines on abdominal segments 3 to 5 or 6 in later stages or in all stages. Lateral knobs on abdominal segments 2 and 3 in all stages. Megalopa with pointed bent rostrum or the rostrum rudimentary, the angles with or without spines. Young crab with emarginate front. Three or four lateral spines to carapace.

Subfamily *XANTHINÆ.*

Four zoeal stages. Zoea with one and two extra pairs of internal setæ on telson in third and fourth zoeæ. Antenna with rudimentary exopodite. All spines present on carapace. Lateral spines on segments 3 to 5 or 6 in later stages. Megalopa with very short notched rostrum bent down; the two angles with or without spines. No dorsal spine on carapace and inconspicuous protuberances. Large hook on ischia of first leg. None on coxæ of legs 2 to 4.

Genus Xantho.

Lateral spines on segments 3 to 5 in later zoeæ. Telson with three lateral spines, the middle one very small and almost disappearing in the last zoea. One pair extra internal setæ in third, two pairs in fourth zoea. Megalopa with a thick spine on each side of rostrum and minute central bilobed spine. *Xantho* can be distinguished from all other British zoeæ by its rudimentary exopodite to the antenna. Cano (1891) describes the various larval stages of a *Xantho*, but does not identify the species. His description and figures agree fairly well with *X. incisus*, but he thinks there are two megalopæ, whilst I find only one. There can be no doubt in the case of *X. incisus*, as it was reared from egg to crab in the laboratory. Hyman (1925), in his review of the larval Xanthidæ, describing *Neopanopæ texana sayi* (Smith), states: "According to Birge, there are four moults during the megalopa stage. The changes at each moult are slight however." And again: "After at least four moults, the megalopa assumes the form of the first crab." It is difficult to be certain from this whether Hyman himself actually saw these moults. He states that he checked over the development on material secured at Beaufort, but adds nothing on this point. It seems likely that there really is only one megalopa, which assumes different aspects when young and old.

Xantho incisus Leach. (Pl. II. fig. 3; Pl. XI. figs. 5–9.)

This crab is common under stones among the rocks at low tide in the district. Berried females in spring and early summer. Very few larval forms are, however, seen in the plankton, zoeæ occasionally in the summer. Eggs were hatched in plunger-jars and all the larval stages and young crab reared. The zoeæ were fed on oyster larvæ; the megalopæ and young crab on pieces of mussel. Unfortunately, the young crab died before moulting any further.

Eggs very dark brown from extrusion to time of hatching, having a speckled appearance just before hatching, owing to the eyes showing through the egg-membrane. Early eggs 0·36 mm., late eggs 0·48 mm. across.

Pre-zoea about 1·5 mm. long, remaining active for some hours before setting free the first zoea.

First zoea about 1·8 mm. long. From spine to spine 1·76 mm. Dorsal spine curved. Colour mainly red and yellow, with blackish-brown chromatophores in the mouth-region, above and below lateral spines of carapace, along intestine and below it, on the basal segments of the maxillipedes, and ventrally on the abdominal segments. The dark pigment is usually accompanied by red, which diffuses into a pale red on eye, lower sides of carapace, and base of maxillipedes, whilst the upper part, base of antennule, and main part of abdomen ventrally are pale yellow. Dorsal and rostral spines, telson, and ends of maxillipedes colourless. Exopodite of antenna rudimentary, with one or two spines; spinous process long. Median lateral spine of telson minute. Short lateral spines on abdominal segments 3 to 5. Rudimentary limbs hidden under carapace.

Second zoea very like the first, but dorsal spine straighter. Length about 1·92 mm. From spine to spine 2·24 mm. Lateral spines longer on abdominal segments 3 and 4. Rudimentary limbs still hidden.

Third zoea about 2·4 mm. long. From spine to spine 2·88 mm. Flagellum of antenna well developed. Rudimentary limbs showing outside carapace. Sixth abdominal segment separated from telson. Pleopods distinct. Lateral spines on segments 3 to 5 longer. Telson with an extra pair of internal spines.

Fourth zoea about 2·8 mm. long. From spine to spine 3·4 mm. Antennule with branch. Antenna with fairly long flagellum, unjointed. Rudimentary limbs larger, but hardly jointed. Spines on abdominal segments 3 to 5 longer. Telson with the middle lateral spine minute. Two extra pairs of internal setæ.

Megalopa with almost square rostrum bent down in the centre into a short bifid tooth, the angles of the rostrum each ending in a strong tooth. Carapace without conspicuous prominences. Last pleopods with ten setæ. Length of carapace 1·36 mm., breadth 0·84 mm.

First Young Crab Stage. Carapace almost round, front indented in the centre. Three denticulated teeth. Colour pinkish-brown. Length of carapace 2 mm., breadth 1·92 mm.

The following dates show the times of changing of one individual from pre-zoea to first crab stage:—

Pre-zoea	17.6.27
First zoea	17.6.27
Second zoea from first.....	22.6.27
Third zoea from second	1.7.27
Fourth zoea from third	11.7.27
Megalopa from fourth zoea...........	18.7.27
First young crab from megalopa ...	8.8.27

It thus took about a month from pre-zoea to megalopa and nearly three weeks from megalopa to crab, the last probably abnormally long.

XANTHO HYDROPHILUS Herbst. (Pl. II. fig. 4.)

Much rarer than *X. incisus*; occurring in the same localities, but usually much further down, so that it can only be collected at extremely low tides. No larvæ of this species have been seen in the plankton. Berried crabs in spring. The pre-zoea and first zoea were obtained from the eggs, but did not live. Gourret (*op. cit.*) gives a figure of the first zoea and telson from Marseilles. Otherwise its life-history is not known.

Eggs dark brown. Late eggs 0·36 mm. across.

Pre-zoea about 1·28 mm. long, soon changing to the first zoea.

First zoea smaller than *X. incisus*, about 0·70 mm. long. From spine to spine about the same. Dorsal spine rather more curved at the tip, but otherwise very like *X. incisus*. Colour pale pinkish-orange with bright red in mouth-region, above lateral spine, along intestine, and at base of maxillipedes. Orange chromatophores along abdomen. Eye black with pinkish-orange. No other black or only a trace.

Subfamily *MENIPPINÆ*.

No extra pairs of internal setæ on telson. Antenna with exopodite nearly as long or as long as the spinous process. All spines present on carapace. Lateral spines on abdominal segments 2 or 3 to 5 or 6 in later stages. Megalopa with pointed rostrum, much bent. No dorsal spine on carapace, but conspicuous prominences. Hook on ischia of first leg. Rudimentary hooks on ischia of second and third, and of coxæ of second, third, and fourth legs.

Genus PILUMNUS.

Lateral spines on all abdominal segments, except first, in later stages Very short dorsal and rostral spines, dorsal much curved. Telson with three lateral spines in all stages. Megalopa without teeth at angles of rostrum. Rostral spine long and sharply pointed, much bent. First young crab stage with front indented in centre. *Pilumnus* can be distinguished at once from *Xantho* in the zoea by its long antennal exopodite. Cano (1891) describes and figures *Pilumnus* sp. in the first, second, and fourth zoea, megalopa (he describes two), and young crab. It is almost certain that the two megalopæ are really only different phases of one, for there is certainly only one at Plymouth. The last zoea changed into the megalopa, and this into the young crab in the laboratory. Cano's species is probably *P. hirtellus*, as the Mediterranean species *P. villosus* and *P. spinife* rare now regarded as varieties of *P. hirtellus* (Milne-Edwardes and Bouvier, 1891). It is interesting, however, to find that Cano's figures show a slightly more advanced development than those from Plymouth, a fact comparable with a former observation (Lebour, 1927) in the Mediterranean and British species of *Maia*.

PILUMNUS HIRTELLUS (L.). (Pl. II. fig. 5; Pl. X. figs. 6–8; Pl. XI. figs. 1–4.)

Common in the district under stones between tide-marks, often found with *Xantho incisus*, and sometimes dredged inside the Sound. Berried crabs in spring and summer, chiefly spring, and larvæ abundant in spring and throughout the summer. The young were reared on oyster larvæ in the laboratory from egg to megalopa, the young crab being obtained from a megalopa from a last zoea taken in the plankton. Williamson (1915) gives original figures of the first zoea.

Eggs dark brown. Early eggs 0·35 mm., late eggs 0·4 mm. across

Pre-zoea about 1·3 mm. long. Moves about for several hours before changing to the first zoea.

First zoea about 1·5 mm. long. From spine to spine 0·96 mm. Dorsal spine about 0·4 mm. long, curved, sometimes, but not always, toothed at the apex. Rostral spine about 0·25 mm. long. Lateral spines very short. Antenna with exopodite nearly as long as the spinous process, spiny. Rudiments of legs present. Carapace edged with fine teeth and long hairs. Abdominal segments denticulated at the hind margins. Lateral spines on second to fifth segments, longest on third. Colour reddish-brown with black chromatophores, accompanied by red at the base of the back of the dorsal spine, mouth-region, base of second maxillipede, along intestine, and ventrally along the abdomen. Some yellow with the red. Main colour reddish-brown.

Second zoea much like first. About 1·8 mm. long. From spine to spine 1·12 mm. Antenna with short flagellum; pleopods just indicated. Margin of carapace and abdominal segments as in first stage. Lateral spine on first segment as well as second to fifth.

Third zoea about 2 mm. long. From spine to spine 1·28 mm. Antennal flagellum and pleopods longer. Sixth abdominal segment separated from telson. Lateral spines on all the segments. Otherwise carapace and abdomen as before. Rudimentary legs larger.

Fourth zoea about 2·5 mm. long. From spine to spine 1·4 mm. Antennule jointed with branch. Rudimentary legs jointed, large. Antennal flagellum and pleopods long. Spines on third and fourth abdominal segments long. Carapace and abdomen otherwise as in third zoea.

Megalopa. Same colouring as zoeæ. Carapace 0·96 mm. long, breadth 0·80 mm. Rostrum fine-pointed, long, bent at an obtuse angle. Conspicuous protuberances on carapace, but no spines. Six setæ on last pleopods.

First Young Crab Stage very small, brownish. Carapace 0·88 mm. long, 1·28 mm. broad. Front indented, hairy. Four sharp lateral teeth at edge of carapace. Two notches in orbit. No further young stages reared.

The following dates show the changes from pre-zoea to megalopa:—

Pre-zoea and first zoea	12.8.26
Second zoea from first	17.8.26
Third zoea from second	23.8.26
Fourth zoea from third	26.8.26
Megalopa from fourth zoea	3.9.26

In this series the growth was quick, less than three weeks being taken to reach the megalopa.

Family GONOPLACIDÆ.

The only British representative of this family is *Gonoplax rhomboides*. As no other species are known in their larval stages, the characters are given under the genus.

Subfamily *GONOPLACINÆ*.

Genus GONOPLAX.

Four zoeal stages. All spines on carapace present. Antenna with pointed exopodite about the same length as the spinous process. Abdomen with knobs on the second to the fourth or fifth segments in all stages, and lateral spines on the third to the fifth in later stages. Telson with two lateral spines in all stages. One and two pairs of extra internal setæ in later stages. Megalopa with broad squarish rostrum without spine. No dorsal spine on carapace and inconspicuous protuberances. Hooks on ischiæ of all legs except last. First young stage very like the adult.

GONOPLAX RHOMBOIDES (L.). (Pl. II. fig. 6; Pl. XI. fig. 10; Pl. XII. figs. 1–4.)

"The Angular Crab" is fairly common in the district on the usual dredging and trawling grounds inside and outside the Sound. Berried crab recorded by Mr. R. A. Todd in June and the young hatched out by him (Plymouth Invertebrate Fauna, 1904), but otherwise no berried crabs seen *. The larvæ are fairly common in the plankton in September and early autumn. These have been kept through various changes, and the young crab reared through several moults from the megalopa and last zoea. The only other record of larval *Gonoplax* is of the megalopa by Cano (1891), but this cannot be the present species, and almost certainly is not a *Gonoplax* at all, having a long dorsal spine which is lacking in *Gonoplax rhomboides*. Cano's specimen might be one of the Canceridæ. The first to the fourth (last) zoeæ and the megalopa were recognized in the Plymouth plankton. They are easily distinguished by their beautiful bright pink colour, unlike any other crab larvæ.

Eggs and *pre-zoea* not available for study.

First zoea about 0·80 mm. long. From spine to spine 0·88 mm. Spines slightly curved. Colour brilliant pink in the mouth-region, diffusing into the lower part of carapace, on rostral spine, at the base of dorsal spine behind, behind and above lateral spines, along the intestine and abdomen, and at the middle joint of maxillipedes. Most of the red masses accompanied by black; eye black. Above the red on carapace and spreading on to the eye it is a diffuse pale yellow and also along abdomen. The zoeæ have fairly long dorsal and rostral spines, short laterals, and antennal exopodite as long as or nearly as long as spinous process, pointed with spines about half-way along. Zoeæ with 4, 6, 8,

---

* See footnote, p. 473.

10 setæ respectively on maxillipedes. Abdomen with knobs on second, third, fourth, and sometimes fifth segments in all stages. Lateral spines on third, fourth, and fifth in all stages, gradually growing longer, and very long in last stage. Telson with two lateral spines in all stages; an extra pair of internal setæ in third and two extra pairs in fourth stage. No pleopods in second; fairly well developed in third and long in fourth stage. Rudimentary legs conspicuous in third and unusually large in fourth stage.

Second zoea much like first. About 1·04 mm. long. From spine to spine 1·2 mm. Antennal flagellum a minute bud.

Third zoea about 2·8 mm. long. From spine to spine 3·2 mm. Antennal flagellum well developed. Pleopods small.

Fourth zoea about 3·6 mm. long. From spine to spine 3·8 mm. Antennal flagellum nearly as long as exopodite and spinous process. Antennule jointed with branch. Mandible with palp. Pleopods long.

Megalopa with squarish rostrum slightly bent, armed with a few hairs. A pair of sharp spines behind eyes. Abdominal segments four and five with lateral spines. Length of carapace 1·68 mm., breadth 1·44 mm. Last pleopods with eight setæ. First leg with large hook on ischia, small hook on mera, second, third, and fourth legs with hooks on coxæ, ischiæ, and basæ, one extra small knob on ischia.

First Young Crab Stage with two lateral teeth on edge of carapace and flat front like adult. Breadth of carapace 2·24 mm. Second young stage 3·8, third 4·9, and fourth 6 mm. The following dates show the times of changing skin:—

Megalopa from last zoeæ	13. 8.26
First young crab stage from megalopa	20. 8.26
Second young crab from first	10. 9.26
Third young crab from second.........	16. 9.26
Fourth young crab from third.........	7.10.26
Fifth young crab from fourth	9.11.26

Family PINNOTHERIDÆ.

Zoea very variable. Antenna a rudimentary stump. Spines of carapace present or absent. A tendency to live near the bottom is shown. Telson variable, three-lobed or forked. Abdominal segments five plus telson in all stages, having a tendency to spread out as they approach the telson. Knobs on second and third abdominal segments in all stages. Two or more zoeal stages. Megalopa without rostrum and without feelers on last joint of last legs.

The two British species are very unlike one another, as has been shown already in a previous paper (Lebour, 1928), and it is very likely that they should be placed in different genera. This is not done here, however, as only the larval stages are dealt with.

Genus Pinnotheres

(as represented by the two British species).

Zoea with or without dorsal spine. Rostral spine and laterals present, but may be reduced. Laterals bending downwards. Two or more zoeal stages. Telson three-lobed, with three setæ each side of central lobe. One or several outer lateral teeth. Megalopa only known in *P. veterum*. Young stages from megalopa not known.

Pinnotheres pisum (Penn.). (Pl. III. fig. 1; Pl. XII. figs. 5-8, 10.)

The "Common Pea Crab" is common inside the mussel (*Mytilus edulis*) in the Plymouth district; it is also recorded from *Modiola vulgaris* and certain ascidians. Berried females in late spring and early summer, rarely in autumn. Zoeæ occasionally in the plankton in summer. Megalopa and young crab stages not known, nor the later zoeæ. This is one of the earliest known crab larvæ, hatched out and figured by Thompson (1835). No further work had been done on it until the present investigations were undertaken and a paper published describing the eggs, pre-zoea, and first zoea (1928). Since then a second (?) zoeal stage was found in the plankton which almost certainly belongs to this species. The pre-zoeæ were hatched out in the laboratory, and changed almost at once to first zoeæ. Unfortunately, the embryonic cuticle was not seen properly, as it is extremely thin and fragile. The first zoeæ did not live to change further, although they fed well on the diatom *Nitzschia*. The zoeæ congregate near the bottom of the aquarium-like *Ebalia*, although when first hatched they keep at the top. They are usually curled up in a ball with the abdomen under the body, and present very little surface for floating.

Eggs bright orange-red changing to brownish. Early egg 0·27 mm., late eggs 0·3 mm. across.

Pre-zoea about 0·80 mm. long, changing almost directly to the first zoeæ.

First zoea about 0·96 mm. long. Colour greenish, made up of black chromatophores accompanied by yellow and a little orange. Eye black with a little yellow. Black chromatophores dorsally, at sides of carapace, in mouth-region, and on abdominal segments, accompanied by yellow and a little orange. No dorsal spine. Rostral spine 0·2 mm., laterals 0·14 mm. long. Carapace egg-shaped, covering traces of rudimentary legs. Abdomen gradually widening towards telson. Telson with three lobes; central lobe longer than outer lobes, which are pointed and denticulated on their outer margin. No trace of pleopods, showing that there must be more than two zoeal stages.

Second zoea (?). This is presumably the second zoea of *P. pisum*, having the same form and colouring. Only one specimen was found in the plankton, and it differs so much in the rostral and lateral spines that it is possible we have here to do with another species, but not likely, or possibly it may be abnormal, but this is not likely, as it looked very healthy and lively. On the whole it seems most probable that it belongs to *P. pisum*. There are six setæ on the maxillipedes, so that it is probably the second zoea, but it might possibly be a third zoea, having, like *Ebalia* and unlike the remaining Brachyrhyncha, the second and third zoeal stages both with six setæ on the maxillipedes. Colour the same as in the first zoea. Length about 1·28 mm. Curled up in a ball. Carapace of the same form as the first zoea, but with rostral and lateral spines much reduced. Rostral spine very short and now quite rudimentary, with three lobes, reminding one of the rudimentary rostral spine in *Ebalia*. Laterals much shorter than in the first stage, not so much bent downwards. Abdomen as in the first stage. Lateral knobs on second and third segment still present. Five segments plus telson, which is of the same form as in the first zoea; outer lobe, however, not so pointed, but still with outside denticles. Pleopods present, well developed, but not long, four pairs with a rudimentary fifth pair showing under telson. From the size of the pleopods this should be a penultimate zoea, indicating that there are probably three zoeal stages, a number so far not found in the crabs. The chief interest of this form is its similarity to *Ebalia*, and seems to show how the *Ebalia* type of rudimentary rostral spine may have been evolved from a longer spine. The similarity between *Pinnotheres* and *Ebalia* larvæ has already been referred to, and this seems to carry it still further.

No later stages are known of this species.

PINNOTHERES VETERUM Bosc. (Pl. III. fig. 2; Pl. XII. figs. 9–11; Pl. XIII. fig. 1.)

The "Pinna Pea Crab" occurs rarely in the district, and was recorded by the earlier naturalists from *Pinna*. In recent years, however, it has not been possible to find it in these molluscs, which are now rare, but it is occasionally found in *Ascidians*. No berried crabs have been seen during the present investigations, but one was found in July 1925 in *Ascidia mentula* which was preserved. Zoeæ occur occasionally in the plankton in late summer and early autumn. This zoea curls up its abdomen under the body as in *P. pisum*, but it does not seem to like the bottom layers better than the others, having a well-developed dorsal spine, the rostral and laterals also being long. First and second zoeæ were both obtained, there being only two zoeal stages in this species. The second came from the first, and the megalopa from a second, zoea, but no young crabs from the megalopæ, which all died after a few weeks. This species is much larger than *P. pisum*, the first zoea being much more advanced. Gourret (*op. cit.*) has figured a zoea which he describes as belonging to the genus *Pisa*, and has also figured the telson of *Pinnotheres* sp. His drawing of *Pisa* is so like the first zoea of

Pinnotheres veterum that it seems almost certain he has mixed the species, and has really figured the zoea of *P. veterum* but the antenna and telson of *Pisa*, whilst his figure of the telson of *Pinnotheres* is almost exactly like that of *P. veterum*.

Eggs orange-red. Early eggs 0·48 mm. across.

First zoea about 1·52 mm. long. Colour pale brownish-red, merging into pale yellow with dark brown chromatophores on dorsal spine, carapace, antennæ, mandible, lateral spines, and abdominal segments. Eyes black. Dorsal spine 0·96 mm. long, slightly curved backwards and then straight. Lateral spines 0·65 mm. long, sticking out behind the body, slightly curved downwards and directed downwards, outwards, and backwards. Rostral spine 0·72 mm. long, slightly curved inwards and outwards. Rudimentary legs hidden by carapace. Abdomen gradually widening towards telson. Pleopods present as small buds on segments 2 to 5. Telson with central lobe shorter than lateral lobe, the latter pointed with a short and thick tooth on its outer margin.

Second zoea very like the first. About 2 mm. long. Six setæ on maxillipedes. Rudimentary legs well developed, but hidden under carapace. Mandible with palp. Pleopods long, four pairs and a rudimentary fifth pair under telson.

Megalopa 1·68 mm. long. Carapace 0·96 mm. long, 0·80 mm. broad. Front with undulating margin slightly projecting in centre. No feelers on last joint of last legs. Abdomen still with only five segments plus telson and four pairs of pleopods developed; the fifth pair rudimentary. Last pleopods with six setæ. This megalopa is very crab-like and swims little, although quite capable of swimming with its pleopods. The abdomen is more often tucked in under the body. Stimpson (see Hyman, 1925) has shown that *Pinnixia sayana* develops into a crab from the zoea without a megalopa stage. Here we seem to have something in between. The similarity between the megalopa of *P. veterum* and *Ebalia* has been noticed before (Lebour, *op cit.* 1928). They are strikingly alike and agree in having no feelers on the last legs, a feature which apparently separates the Brachyrhyncha from the Oxyrhyncha, with this one exception. *Pinnotheres* is certainly a near relative of the Grapsidæ and must belong to the Brachyrhyncha. *Planes*, a grapsoid described in its zoeal stages by Hyman (1926), is like *Pinnotheres* in many ways. Further work on foreign forms should bring out interesting results.

OXYSTOMATA.

Family LEUCOSIIDÆ.

Subfamily *LEUCOSIINÆ*.

Zoea curling up in a ball. No dorsal spine; rostral and lateral spines rudimentary or the rostral well developed and laterals

bending downwards. Carapace more or less egg-shaped. Antennæ rudimentary stumps. Telson a triangular plate, emarginate behind, with six setæ in the centre of the emarginate portion and one or more teeth at or near the angles.

Genus EBALIA.

Four zoeal stages, the second and third each having six setæ on the maxillipedes, the fourth eight. Pre-zoea with forked telson covered with the usual seven embryonic spines on each side; antennule and antenna each with two long spines. Zoea with rudimentary rostral and lateral spines. Abdomen with five segments plus telson in all zoeal stages; four pairs of pleopods, the fifth rudimentary under telson. Knobs on second and third abdominal segments in all stages. Telson with one or more teeth at or near the angles. Megalopa without rostrum, the centre of front slightly projecting. No spines on carapace and very inconspicuous protuberances, except a central dorsal hump behind. Abdomen with six segments plus telson and five pairs of pleopods. Last legs without feelers on last joint.

EBALIA TUBEROSA (Pennant). (Text-fig. 2, 3–6; Pl. III. fig. 3; Pl. XIII. figs. 10–13; Pl. XIV. fig. 1.)

"Pennant's Ebalia" has already been described in its larval stages in a former paper (Lebour, 1928). This is the commonest *Ebalia* in the district, occurring in the sand both inside and outside the Sound, and frequently dredged. Berried females from January to late summer or autumn. Larvæ in the plankton nearly all the year round, chiefly in spring and summer and chiefly from near the bottom. Pre-zoeæ and first zoeæ were obtained from the eggs, but these did not live, and later larvæ from the plankton were reared to megalopæ and young crabs. Williamson (1914) describes and figures certain stages of a larval *Ebalia*, unspecified, which is almost certainly this species. Miss Jörgensen's (1923) are also almost certainly chiefly *E. tuberosa*. She has kindly sent some specimens which agree exactly with these, but amongst them is anothor species which must be *E. cranchii*, as the third British species *E. tumefacta* apparently does not occur on the coasts of Northumberland.

Eggs dark orange-red. Early eggs 0·28 mm., late eggs 3 mm. across.

Pre-zoeæ about 1·28 mm. long, quickly changing to first zoea.

First zoea about 1·28 mm. long. Colour red, orange, yellow, and black, not so much red in the first stage, but very conspicuous in later stages in the lower part of thorax. Orange spot dorsally with black. Much black mixed with red and diffuse yellow on carapace, mouth-parts, and ventrally along abdomen. Rudimentary rostrum with three teeth; lateral spines rudimentary, at first rounded knobs, but in later stages projecting horizontally outwards as short spines. Carapace at first covering rudimentary limbs, which project in later stages. Telson with one tooth just behind angle of plate; the angle rounded.

Second zoea about 1·6 mm. long. Six setæ on maxillipedes. No pleopods.

Third zoea about 1·9 mm. long. Six setæ on maxillipedes. Pleopods present as conspicuous buds.

Fourth zoea about 2 mm. long. Pleopods long.

Megalopa 2·2 mm. long. Deep red with yellow and a little black. Six setæ on last pleopods.

First Young Crab Stage light brown, very like adult, with emarginate front to carapace. Length of carapace 1·6 mm.

EBALIA CRANCHII Leach. (Pl. III. fig. 4; Pl. XIII. figs. 4–9.)

"Cranch's Ebalia" occurs in much the same places in the district as *E. tuberosa*, but is not so common. Berried females occur in spring and probably in the summer, but were not hatched out. Larvæ from the plankton almost certainly belong to this species, as they correspond exactly with some of those sent by Miss Jörgensen from the Northumberland coast, and as *E. tumefacta* does not occur there, this identification is almost certainly correct. All four zoeæ occurred which, like *E. tuberosa*, have the second and third stages both with six setæ on the maxillipedes. Cano (1892) has figured the zoea of *E. cranchii*, at first calling it *Plagusia*, afterwards correcting it to *Ebalia* sp. It is recognizable by the telson, which has three teeth at the angle, and by this character is easily distinguished from *E. tuberosa*. The megalopa was reared at Plymouth from the zoea, but the young crabs were not obtained

Eggs orange-red; half developed, 0·28 mm. across.

First zoea about 1·12 mm. long. Colour pinkish with a little yellow, an orange and black chromatophore dorsally each side of carapace, black on the maxilla, abdominal segments, and over the intestine, red below. Not nearly so much red in the later stages as in *E. tuberosa*. All larval stages smaller than in *E. tuberosa*. Rostral spine rudimentary, faintly divided into two. No lateral spines in any stages, these being represented by rounded prominences.

Second zoea about 1·28 mm. long. No pleopods.

Third zoea about 1·7 mm. long. Pleopods present as small buds. Rudimentary legs well developed.

Fourth zoea about 1·92 mm. long. Rudimentary legs large. Pleopods long (four pairs, the fifth pair projecting, from telson). Still only five abdominal segments plus telson.

Megalopa 1·8 mm. long. Very like that of *E. tuberosa*, but smaller, not so red, and with four setæ on the last pleopods. First young crab stage not obtained.

The third species, *E. tumefacta*, occurs in the district, but is rare, and the larvæ were not certainly identified.

Gurney (1927) figures two zoeæ of *Leucosia* which are very like *Ebalia*. The earlier stage has fairly prominent rostral and lateral spines, which remind one of *Pinnotheres pisum*. The later stage has much smaller spines. If these be the same species we have a similar reduction.

OXYRHYNCHA.

The following characters apply to all the British forms, including *Eurynome* *.

Pre-zoea with the usual seven embryonic spines on each side of telson, two on antennule and four on antennæ, with simple sheaths for spinous process and flagellum. Two zoeal stages, one megalopa. First zoea far forward in development, showing antennal flagellum and pleopods. Lateral spines on abdominal segments 3 to 5. Horns of fork of telson with spicules. Megalopa with rostrum, without feelers on last joint of last leg.

As a rule the megalopa stage is reached in a fortnight or less, about five days being taken to reach the second zoea. The young crab in favourable circumstances should emerge from the megalopa in about three weeks from hatching.

Key to the Genera of the Oxyrhyncha.

ZOEÆ.

I. Dorsal spine only on carapace. No rostrals nor laterals.	
1. Large lateral spine on telson	*Inachus.*
2. Small lateral spine on telson	*Macropodia.*
II. Dorsal and rostral spines on carapace. No laterals	*Eurynome.*
III. All spines present on carapace.	
1. Carapace spines armed with spicules	*Hyas.*
2. Carapace spines smooth	*Maia.*

MEGALOPÆ.

I. Seven abdominal segments, five pairs of pleopods.	
1. Rostrum three-toothed	*Hyas.*
2. Rostrum broad, with pointed bent-down spine.	
a. Five setæ to last pleopods	*Maia.*
b. Three setæ to last pleopods	*Eurynome.*
II. Six abdominal segments, four pairs of pleopods.	
a. Rostrum with two horns	*Inachus.*
b. Rostrum bent, forming three rounded lobes	*Macropodia.*

Family MAIIDÆ.

Subfamily *MAIINÆ.*

Zoea with antennal exopodite about half as long as, or rather more than half the length of, the spinous process. Flagellum

---

* If Cano's (1893) descriptions be correct, certain members of the Parthenopidæ have larvæ which are more like Brachyrhyncha and certainly differ in important particulars from *Eurynome*.

well developed. Spines of carapace short, laterals present or absent, dorsal and rostral curved. Lateral knobs on second abdominal segment only. Six abdominal segments in first, seven in second zoea (five and six plus telson). Telson with three lateral spines in both stages; one pair extra internal setæ may or may not be present in second stage. Megalopa with broad rostrum ending in pointed bent-down spine; knobby protuberances on carapace but no spines. First young crab stage with pointed rostrum or two horns.

Genus MAIA.

All carapace spines present. Telson without any extra internal setæ in second zoea.

MAIA SQUINADO Herbst. (Text-fig. 2, 1–2 & Pl. II. fig. 7; Pl. XIV. figs. 6–7.)

The "Spinous Spider-Crab" is very common on the trawling grounds both inside and outside the Sound. Berried females in spring and summer, but chiefly summer. Larvæ in the plankton abundant in late summer. The larvæ were reared from the egg as far as the megalopa, the crab being obtained from megalopæ from plankton zoeæ. An account of the life-history of this species has already been given (Lebour, 1927). Schlegel (1911) had reared it from egg to crab at Roscoff, but gave no details of his methods and no figures. Claus (1876) figures the zoea of a *Maia*. Cano (1893) describes and figures the Mediterranean species *M. verrucosa*, which is further developed than *M. squinado* in the corresponding stages.

Eggs bright orange, changing to nearly black when ready to hatch. Early eggs 0·64 mm., late eggs 0·72 mm. across.

Pre-zoea about 2·5 mm. long, remaining for some hours in the embryonic skin and moving actively before changing to the first zoea.

First zoea about 2·5 mm. long. From spine to spine 1·76 mm. Colour green, made up of black and yellow. Diffuse yellow all over, except on spines of carapace, telson, and ends of maxillipedes, which are colourless. Eye black with yellow. Black chromatophore at base of dorsal and rostral spines, several on carapace, at sides of base of maxillipedes, along intestine and ventrally along abdomen, always accompanied by yellow. Both rostral and dorsal spines curved. Long hairs at edge of carapace. Short lateral spines on abdominal segments 2 to 5.

Second zoea about 3 mm. long. From spine to spine 1·8 mm.; dorsal spine much shorter than in first zoea. No palp on mandible. Antennule and rudimentary legs unjointed. Pleopods long. Lateral spines on abdominal segments 3 to 5 longer.

Megalopa same colour as zoea. Length 2·4 mm. Rostrum broad, indented in the centre and with a very fine central spine bent down and almost concealed. Large protuberances on carapace. Five setæ on last pleopods.

First Young Crab Stage 1·28 mm. across carapace. Light brown, covering itself at once with any débris it can find. Carapace roundish. Front pointed, five lateral marginal teeth, legs rather short. Second young stage 1·9 mm. across carapace, third young stage 2·5 mm. All with pointed rostrum, crenulated at margin.

Genus EURYNOME.

Telson with a pair of extra internal spines in the second zoea. No lateral spines on carapace. First young crab stage with two rostral horns.

EURYNOME ASPERA Leach. (Pl. II. fig. 8; Pl. XIV. figs. 2–5.)

Common in crevices of stones and polyzoa in the Sound and outside. Berried females in spring and summer. Larvæ in the plankton common in spring and summer, more rarely in autumn. Pre-zoea and first zoea hatched from eggs, but did not live. Second zoea from plankton changed to megalopa, and this to first young crab. No later young crab stages. Cano (1893) figures the first zoea and Kinahan (1857) the pre-zoea. Gurney (1922) also describes these stages and figures the pre-zoeal spines.

Eggs bright red, clear and of a darkish shade. Early eggs 0·36 mm., late eggs 0·37 mm. across.

Pre-zoea about 1·67 mm. long, soon changing to the first zoea.

First zoea about 1·6 mm. long. From spine to spine 1·4 mm. Spines curved. Antennal exopodite like *Maia*, about half the length of the spinous process; flagellum well developed. Long hairs at edge of carapace.

Colour orange and brown, with black chromatophores on base of dorsal spine at back, in mouth-region, on carapace, base of maxillipedes, along intestine and ventrally along abdomen. Dark reddish-brown above mouth, orange merging into yellow and pinkish on carapace, abdomen, and base of maxillipedes. Tips of spines, telson, and maxillipedes colourless.

Second zoea about 1·92 mm. long. From spine to spine 15·2 mm. Pleopods well developed except last, which is small.

Megalopa with pointed central spine to rostrum bent down at a right angle; the sides rounded. Conspicuous protuberances on carapace. Length of carapace 5 mm., breadth 0·4 mm. Last pleopods with three setæ. Same colour as zoeæ.

First Young Crab Stage. Pale brownish. Two-horned rostrum, very knobby carapace Length of carapace 2 mm., breadth 1·2 mm. The larval stages of *Eurynome*, including the megalopa, are very like *Maia*, and they are placed here in the same family and subfamily instead of in the Parthenopidæ.

Subfamily *PISINÆ*.

This subfamily includes *Pisa* and *Hyas*. It seems very doubtful, however, whether these two genera should be placed in the same subfamily, as the only existing descriptions of the larval stages of *Pisa* are quite unlike *Hyas*. The subfamily is left as it is, because the larvæ of *Pisa* have not been seen at Plymouth, and these should be very carefully examined before any alterations are made.

Genus PISA.

PISA BIACULEATA (Montagu).

This is rare in the Plymouth district, and whilst these investigations were proceeding has only once been found in berry, in July 1926. Unfortunately these eggs did not live; they measured 0·72 mm. across. Cano (1893) figures the zoeæ, megalopa, and young crab stage of *Pisa*. The zoea is very like *Inachus*, but has six abdominal segments plus telson in the second zoea and megalopa. There are neither rostral nor lateral spines, and the antennæ have a long exopodite similar to *Inachus*. The whole appearance is like one of the Inachinæ. Gourret (*op. cit.*) figures the first zoea of *Pisa*, but this is almost certainly *Pinnotheres veterum*. His figures of the telson and antenna, however, show them to be of the *Inachus* type. It is very desirable that more investigations should be made on the larvæ of *Pisa*.

Genus HYAS.

All spines present on carapace and all covered with spicules. Antennal exopodite less than half the length of the spinous process; flagellum very small in first zoea. Lateral knobs on second and third abdominal segments in both stages. Telson with two lateral spines in both stages; a pair of extra internal setæ in second zoea. Long lateral spines on third to fifth segments in both stages. Megalopa with three-toothed rostrum; dorsal spine behind and two horns behind eyes. Hooks on coxa of second to fourth legs. First young crab stage with two-horned rostrum

HYAS COARCTATUS (Leach). (Pl. II. fig. 9; Pl. XIV. figs. 8–10.)

Fairly common both inside and outside the Sound on the trawling and dredging grounds. Berried females from March to December. Larvæ in the plankton chiefly in early spring. Reared from egg to first zoea, but these did not live. Second zoea from the plankton. Megalopa from the plankton changed to young crab. As the megalopa did not come from the zoea, it is not absolutely, but almost, certain that these belong to *H. coarctatus*. It is much more probable than their belonging to *H. araneus*, which is now very rare. These megalopæ occur at the same time as the zoeæ of *H. coarctatus*, and are of much the same colour. No others have been seen, and it is highly unlikely that the rarer form only should be found. It is therefore inferred, though recognized as not proved, that this megalopa belongs to *H. coarctatus*.

Eggs bright orange, changing to an orange-brown. Early eggs 0·4 mm. across, late eggs 0·56 mm.

Pre-zoea about 0·92 mm. long, moving about for some time before changing to the first zoea.

First zoea about 1·8 mm. long. From spine to spine 3 mm. Spinous process of antenna long, nearly as long as the rostral spine; exopodite less than a third of the length of the spinous process; flagellum very small. Long hairs at border of carapace. Colour brownish, chiefly in the thoracic region. Spines of carapace colourless: eye brownish-black with red pigment internally; orange spot at hind base of dorsal spine, diffuse yellow in front and dorsally; dark brown accompanied by red under intestine and on ventral surface of abdomen; red at base of antennæ; red and brown on base of first and second maxillipedes.

Second zoea about 3·5 mm. long. From spine to spine 3·52 mm. Long hairs on edge of carapace. Antennal flagellum well developed, unjointed. Antennule slightly jointed. Rudimentary legs not very well developed

Megalopa much the same colouring; 3·36 mm. long. Carapace 2·4 mm. long, 0·96 mm. broad. Central rostral tooth about twice as long as the lateral teeth. Last pleopods with five setæ.

First Young Crab Stage 2 mm. long, with two-horned rostrum. Sides of carapace very irregularly denticulated. No further young stages.

Stephenson (1913) has partly described the larvæ of this species; also Björk (1913), who figures the megalopal rostrum and part of carapace. Williamson (1914) describes larvæ from Greenland which were collected by Van Höffen and Trasing. These are considerably larger than Williamson's own specimens, attributed to *H. araneus*, and also than those from Plymouth. They seem, however, to belong to this species.

HYAS ARANEUS (L.).

Although this crab is recorded from the district, it has not been found at all during the period of these investigations, and no larvæ attributable to this species have been seen. Judging from the description by Williamson (1909, 1914), they are exceedingly like those of *H. coarcticus*.

Subfamily *INACHINÆ*.

Zoea with dorsal spine to carapace, but neither rostrals nor laterals. Antenna with spiny exopodite, as long as, or nearly as long as, the spinous process; flagellum well developed. Abdomen with six segments (five plus telson) in all stages, both zoea and megalopa, and only four pairs of pleopods. Lateral knob on

second abdominal segment only. Telson with only one lateral spine and no extra pairs of internal setæ. Megalopa with pronounced rostrum and spines or long prominences dorsally on carapace. Many hooks on legs.

Genus INACHUS.

Telson of zoea with very large lateral spine. Megalopa with two rostral horns sticking out horizontally. Prominences on carapace low and finely pointed, forming prickly spines. The three British species of *Inachus* are very much alike both in zoeæ and megalopæ, and it is extremely difficult to separate them in the plankton.

INACHUS DORSETTENSIS (Pennant). (Pl. III. fig. 5; Pl. XV. figs. 4–5.)

The "Scorpion Spider-Crab" is very common in the district, the commonest of all the Inachinæ. It occurs both inside and outside the Sound, chiefly outside, on the usual trawling grounds. Berried females occur all the year round, and larvæ are to be found in the plankton in any month, perhaps specially abundantly in autumn. This species has already been described in its larval stages (Lebour, 1927), and was reared from egg to megalopa. Since then it has been reared successfully as far as the seventh young crab stage. Claus (1876) figures the first zoea, and also Cano (1893). Otherwise it was not described further until these researches were begun.

Eggs orange-red; early eggs 0·48 mm., late eggs 0·72 mm.

Pre-zoea about 1·9 mm. long; living for several hours before changing to the first zoea.

First zoea about 2·4 mm. long. Carapace bordered by small denticulations. Colour yellow with black and orange. Body pale yellow almost all over; most of dorsal spine colourless, also tips of antennule, antennæ, maxillipedes, and telson. Eye blackish-brown with splashings of yellow; yellow tends to become orange in region of stomach. Bright orange-red chromatophores at base of dorsal spine posteriorly, the sides of the first abdominal segment, between eyes, on mandible, above the maxillipedes and on the second maxillipede, and a diffuse pinkish tinge round the fore part of body under carapace. Blackish-brown chromatophores, with the red at base of spine, between eyes, separately on the carapace and ventrally on the abdominal segments and base of telson.

Second zoea about 2·9 mm. long. Much like the first, but with long antennal flagellum and long pleopods. Dorsal spine shorter. Antennule and rudimentary legs unsegmented. No mandibular palp.

Megalopa 1·6 mm. long. Colour chiefly yellow with brown, black, and red. Legs long and slender with very pointed tips. Width with outstretched legs about 2·5 mm.

First Young Crab Stage 0·96 mm. across carapace, bicornuate rostrum, long legs with one thick thorn-like hook on the last segment of the last two legs. Three knobs behind the eyes, two large round prominences behind.

Second Young Crab Stage 1·28 mm. across carapace. Last two legs with two thorns on last segment.

Third Young Crab Stage 2 mm. across carapace. The young crab begins to dress up directly it has left the megalopal skin. In this case pieces of débris and old larval oyster-shells were used, the crab being almost hidden by a fluffy covering. The most successful food for the zoeæ was oyster larvæ in an aquarium where there was a good deal of green food (chiefly the flagellate *Phæocystis* and diatoms). The megalopæ and young crabs were fed on pieces of the mantle of the common mussel. The following notes give the dates of all the stages:—

Pre-zoea from egg	12. 6.27
First zoea from pre-zoea	12. 6.27
Second zoea from first	16. 6.27
Megalopa from second	23. 6.27
First young crab from megalopa ...	4. 7.27
Second young crab from first	15. 7.27
Third young crab from second	26. 7.27
Fourth young crab from third	8. 8.27
Fifth young crab from fourth	17. 8.27
Sixth young crab from fifth	1. 9.27
Seventh young crab from sixth ...	1.10.27

It is thus seen that it takes about three weeks to reach the crab stage, after which the skin is cast at frequent intervals which gradually grow longer, the first castings being at about intervals of eleven days, later taking about a month. At the seventh stage the crab is well grown, having a breadth with legs out-stretched of about 5 cm.

INACHUS DORYNCHUS Leach. (Pl. III. fig. 6; Pl. XIV. fig. 12; Pl. XV. fig. 3.)

This species and the following one, *I. leptocheirus*, have usually been confused in this district. They are, however, quite distinct, the present species being much smaller and inhabiting the inshore waters, *I. leptocheirus* living a good deal further out. The larvæ are much alike, although in the true *I. dorynchus* they are usually smaller; but the size may vary much, and some of those reared are of just the same size as those of *I. leptocheirus*. The second zoea is actually at times smaller than some of the first zoeæ; and here a second zoea has been figured which was reared and is smaller than the first zoea figured, which came from a different family. It is practically impossible to distinguish the zoeæ in the plankton, although, generally speaking, those of *I. leptocheirus* are brighter and more conspicuously coloured than those of *Dorynchus* and usually larger. *Inachus dorynchus* occurs chiefly inside the Sound, and is commonest near the coast, where it is frequently dredged. Berried females occur all the year round, and larvæ are apparently in the plankton most of the year, all the *Inachus* species being specially abundant in autumn. This species was reared from egg to megalopa, the young crab being obtained from megalopæ from the plankton, but unfortunately died, so that no drawing was made of it. Gourret (*op. cit.*) figures the pre-zoea of this species. Otherwise nothing was known of its larvæ.

Eggs bright orange-red, changing to pale brownish. Early eggs 0·65 mm. across, late eggs 0·72 mm.

Pre-zoea about 2 mm. long, moving about for some hours before changing to the first zoea.

First zoea about 1·8 to 2·4 mm. long. Same colouring as *I. dorsettensis*, slightly more brightly coloured in some specimens, paler in others. Dark chromatophores more brown than black. More brown on the telson, no dark chromatophore at base of dorsal spine. Dorsal spine and antenna rather longer than in *I. dorsettensis*. Lateral spine of telson about the same as in *Dorsettensis*.

Second zoea about 2 to 25 mm. long. Dorsal spine shorter than in first zoea. Pleopods long. Antennules and rudimentary legs hardly jointed. No mandibular palp. Antennal flagellum well developed.

Megalopa much like *I. dorsettensis*. Carapace 0·88 mm. long. Eight setæ to all pleopods as in *I. dorsettensis*. Outstretch of legs longer, about 4·5 mm. across. Rostral horns rather closer together.

First Young Crab Stage not measured. Very like the other two species.

INACHUS LEPTOCHEIRUS Leach. (Pl. III. fig. 7; Pl. XIV. figs. 11, 13; Pl. XV. figs. 1, 2.)

The largest species of the three, inhabiting deeper water outside the Sound. Common sometimes in the trawl, and may occur with *I. dorsettensis* but never with *I. dorynchus*. Berried females all the year round. Larvæ probably in the plankton all the year round, but not always distinguished from the others. They are usually larger and brighter-coloured than the other two. This species was reared from egg to second zoea only, the second zoea from the plankton changing to the megalopa, and this to the young crab. No previous work has been done on the larval stages.

Eggs bright orange-red, changing to brownish. Early eggs 0·65 mm., later eggs 0·80 mm. or more.

Pre-zoea about 2·4 mm. long, moving about for some hours before freeing the first zoea.

First zoea about 2·4 to 2·8 mm. long. Very like *I. dorynchus*, but usually brighter in colour. Lateral spine of telson longer than in the others.

Second zoea about 3 mm. long. Dorsal spine very small; very like *I. dorynchus* and backward in development.

Megalopa larger than *I. dorynchus*. Length of carapace 1·25 mm. Eight setæ to pleopods like the others. Deeper colour, brighter and more spiny than in the other two. Outstretch of legs about 4·6 mm. Rostral horns like *I. dorynchus*, nearer together than in *I. dorsettensis*.

First Young Crab Stage with two-horned rostrum. Very hairy carapace 0·80 mm. across, 0·16 mm. long, with knobs similar to the first stage of *I. dorsettensis*. Very long legs.

Genus Macropodia.

Telson of zoea with small lateral spine. Megalopa with three-lobed rostrum, the centre bent down and sometimes almost hidden. Prominences on carapace prolonged into tall processes. The three species of *Macropodia* are much alike, especially *M. rostratus* and *M. egyptia*, but they can all be distinguished from one another. Large hook on ischia of legs 2 and 3. Several other smaller hooks.

Macropodia longirostris (Fabricius). (Pl. III. fig. 8.)

The "Slender Spider-Crab," the commonest species of the genus. Occurs inside and outside the Sound in the usual trawling grounds. It is the only species of the three to occur in deeper water. Berried crabs all the year round and larvæ in the plankton all the year round, chiefly in spring and early autumn. This species has already been described in all its larval forms in a previous paper (Lebour, 1927). It was reared from egg to megalopa in the laboratory, the young crabs being obtained from megalopæ from second zoeæ collected in the plankton.

Eggs bright orange-red, turning to brownish. Early eggs 0·55 mm., late eggs 0·6 mm. across.

Pre-zoea about 2·4 mm. long, moving about for some hours before changing to the first zoea.

First zoea about 2·7 mm. long. Very like all the *Inachus* species in colouring, but with more dark pigment on the abdomen. No red at base of dorsal spine. Antennæ and dorsal spine long, but not nearly so long as in the other two species. Dorsal spine curved.

Second zoea about 3 mm. long. Dorsal spine shorter. Antennæ about the same length. Backward in development, with antennule and legs hardly jointed and no mandibular palp. Pleopods long.

Megalopa 2·3 mm. long, with very long legs. Front of carapace bent down so that the lobes hardly show and an almost straight margin is seen. Colour dark chestnut, speckled.

First Young Crab Stage 1·2 mm. across carapace. Legs with stretch of over a centimetre. Last legs with five or more teeth on the last joint. Rostrum bilobed, each lobe squarish with three lateral prominences, and, as well as the body and legs, armed with long curved hairs.

MACROPODIA ROSTRATUS (L.) (Pl. III. fig. 10; Pl. XV. fig. 7; Pl. XVI. figs. 3, 5, 8.)

The "Long-legged Spider-Crab" is common in the shallower waters of the Sound, and is often found in the dredgings covered with red or green weed. It is in berry all the year round, and larvæ are apparently to be found in the plankton almost at any time, but especially in spring and early autumn. Cano (1893) has figured the first zoea, megalopa, and first crab stage with details of the parts. Lo Bianco (1904) figures the first crab stage. No further work has been done on this species. Eggs were hatched and the larvæ reared as far as the megalopa in the laboratory. Megalopæ from second zoeæ collected from the plankton were kept until they changed into young crabs. *M. rostratus* and *M. egyptia* are much alike in their larval stages, and can be distinguished easily from *M. longirostris* by their long straight spines and colouring.

Eggs orange-red. Early eggs 0·45 mm., late eggs 0·58 mm. across.

Pre-zoea about 1·76 mm. long, moving about for some time before changing to the first zoea.

First zoea about 1·9 mm. long. Long straight dorsal spine about 1 mm. long; antennæ long, 0·76 mm. It has the same scheme of colouring as *Inachus* and *M. longirostris*, but not so yellow, the yellow mostly replaced by pinkish or pinkish-brown. Red at base of dorsal spine and a good deal of black. On the whole paler than *M. longirostris*.

Second zoea about 3 mm. long. Dorsal spine much the same, antennæ slightly shorter. Long pleopods. Not so far advanced as *M. longirostris*, having no trace of jointing in antennule, antennal flagellum, and legs.

Megalopa 1·76 mm. long. Legs not so long as in *M. longirostris*. Rostrum not so bent so that the three lobes are seen. Colour pinkish-brown, speckled.

First Young Crab Stage 0·96 mm. across carapace. Stretch of legs about 6 mm. Last legs with three thorns on the last joint. Rostrum two-lobed, with deep median indentation. Sides of lobe a simple curve.

MACROPODIA EGYPTIA A. Milne-Edwards. (Pl. III. fig. 9; Pl. XV. fig. 6; Pl. XVI. figs. 1–2, 7.)

This species is not so common as the other two, and its larval stages have not been described before. It occurs in shallow water in the Sound in the same localites as *M. rostratus*, usually also dressed up in green or red weed. Berried females seem to occur at any time of year, and larvæ are apparently in the plankton all the year round, most frequently in spring and summer. The larvæ have been reared from egg to second zoea. Megalopæ from second zoeæ from the plankton were kept until the young crabs emerged. The larvæ are very like *M. rostratus*, but can be distinguished by their longer antennæ.

Eggs orange-red. Early eggs 0·48 mm., late eggs 0·58 mm. across.

Pre-zoea about 1·76 mm. long, moving about for some time before giving rise to the first zoea.

First zoea about 0·24 mm. long. Dorsal spine nearly straight, 1 mm. long, about the same length as in *M. rostratus*. Antennæ about 1 mm. long. Colour very like *M. rostratus*, with slightly more dark pigment. Otherwise very like *M. rostratus*.

Second zoea about 1 mm. long, not or hardly larger than the first. Dorsal spine and antennæ shorter. Advanced at about the same degree as *M. rostratus*.

Megalopa hardly to be distinguished from *M. rostratus*. Much the same colouring. Rostrum with central lobe protruding more, slightly larger.

First Young Crab Stage. Carapace about the same size as *M. rostratus*, stretch of legs longer. Last legs with four thorns on the last joint. Rostrum not so deeply cleft, each lobe divided into two rounded lobes.

Genus ACHÆUS.

The larvæ of *Achæus cranchii*, the only British species of the genus, are not known. In a berried female found by Mr. O. D. Hunt amongst rocks at low tide at Wembury in April 1922 the eggs measured 0·72 mm. across. They are thus very large for such a small crab.

FURTHER WORK ON THE LARVAL STAGES OF SOME FOREIGN CRABS.

Besides the British species a certain amount of work has been done on foreign forms, and these, as a rule, fit in well with the schemes given above. In some cases the correctness of identification is uncertain, but when the zoeæ are actually obtained from the berried crab the results, when placed together with the British species, form a natural system, so that the genus of almost any crab can be identified.

The chief workers on foreign crabs which do not occur in Britain are Cano in Italy and several from America, including Faxon, Smith, Hyman, and Conolly. Many of Cano's species are not identified, and these may or may not be British forms. Some of them are, however, almost certainly British (*Pilumnus*, *Xantho*, *Inachus*, and *Macropodia*).

The families are taken in order as arranged by Calman (1907).

Oxystomata. Family DORIPPIDÆ.—Cano (1891) describes the larvæ of *Dorippe*, *Cymopolia*, and *Ethusia*. These are so peculiar that they could be recognized anywhere, and are not in the least like other crab zoeæ, having very long carapace spines, long abdomen, and long telson with very few setæ. Gurney (1924) figures what is apparentiy a *Dorippe* zoea from the 'Terra Nova' Expedition. Cano (1893) shows the megalopa of *Dorippe* to have feelers on the last joint of the last legs, and in the zoeæ of all these forms the antennæ are well developed, thus differing completely from *Ebalia* and *Leucosia*. Gurney (1927) figures zoeæ of *Leucosia* which are very like *Ebalia*. Cano's (1891) zoeæ, attributed to *Ilia*, he afterwards found belonged to *Pilumnus* (1903), when he figured the telson of the true *Ilia*, which is like *Ebalia* and *Leucosia*.

Brachyryncha. Family PORTUNIDÆ.—Cano (1882) describes *Lupa*, but in most cases does not separate it from *Portunus*. He figures the first zoea, which is very like *Portunus*.

Family POTAMONIDÆ.—Several authors heve described young belonging to crabs of this family as having no true larval stage, but emerging from the egg very like the adult (see Moreira, 1912).

Family CANCRIDÆ.—Conolly (1923) has described the larval stages of *Cancer amœnus*, which has all the characters of the genus *Cancer* but only four zoeal stages.

Family XANTHIDÆ.—Cano's (1891) larvæ of *Xantho* and *Pilumnus*, not identified, are almost certainly British species. Hyman (1925) gives a summary of all larvæ of the family so far described. These divide naturally into two groups, one, to which *Xantho* belongs, having a rudimentary antennal exopodite, and the other, to which *Pilumnus* belongs, having a well-developed exopodite. Cano, in describing *Eriphia*, shows a third type with antennæ like *Portunus*. Hyman places this genus with *Pilumnus*, but it should certainly be in a separate subfamily if the larvæ be correctly identified. Hyman describes *Neopanope texana sayi*, which was originally investigated by Birge, in all four zoeal stages, megalopa, and young crab. This fits in well with the *Xantho* group. Faxon (1880) figures and describes the first zoea. Conolly (1925) describes all the larval stages of *Rhithropanopeus harrisi*, and Hyman also describes the *Eurypanopeus depressus*, *Panopeus herbsti*, which are very like *Neopanope*, and the pre-zoea of *Hexapanopeus angustifrons*. All of these agree well with the *Xantho* group. In the *Pilumnus* group he describes *Menippe mercenaria* in the pre-zoea and first zoea, but this should probably be placed with *Eriphia* in the Eriphiinæ, as its antennæ resemble *Portunus* and neither *Xantho* nor *Pilumnus*.

Family GONOPLACIDÆ.—Cano (1893) describes zoeæ and megalopa of *Brachynotus sexdentatus.* The zoeæ have all the carapace spines, antennæ like *Portunus*, knobs on second abdominal segment only, and lateral spines on the third to fifth abdominal segments in the later stages. The megalopæ figured resemble the figure given of *Gonoplax*, but this does not really belong to *Gonoplax*, as shown above. The zoeæ of *Brachynotus* differ from the true *Gonoplax* in the antennæ.

Family PINNOTHERIDÆ.—Hyman (1924) gives a summary of the larval Pinnotheridæ known, with an account of some of his own work on this most interesting family. All agree in having a rudimentary antenna; otherwise they are very variable. He describes the first and second zoea of *Pinnotheres ostreum*, which closely resembles *Pinnotheres pisum*, and the first zoea of *Pinnotheres maculatus*, which has all the carapace spines and a forked telson with six internal setæ but no lateral spines, the forks being covered with spicules. There are the usual two pairs of knobs on the second and third abdominal segments. This crab, judging from the larva, should probably be placed in a separate genus or else in the genus *Dissodactylus*, for it closely resembles the larva *Dissodactylus mellitæ*, except for a peculiar protuberance which that species has dorsally on its first abdominal segment. This first zoea is described by Hyman, also that of *Pinnixia chætopterana*, which has all four carapace spines and a very peculiar telson with central lobe and forks with spicules. Smith (1880) obtained the megalopa from the last zoea, but gives no description or figure. *Pinnixia sayana* in its last zoea is described by Faxon (1879), who found that it moulted directly into a young crab without any megalopal stage. Gurney (1924) figures a zoea which is almost certainly a *Pinnixia*, the telson closely resembling that of *P. sayana.*

Family GRAPSIDÆ.—Hyman (1924) gives a summary of all the known larval forms of this family. All these lack lateral spines on the carapace, and have fairly long antennæ about the same length as the rostral spine. He describes the first zoea of *Planes minutus*, which is very minute. The antennæ has a long spinous process and very small exopodite with one hair. There are pronounced lateral tubercles on the abdominal segments 2, 3, and 4 which recall *Gonoplax*. The telson is of the typical forked form, but the forks are covered with spicules and there is one lateral spine. This zoea suggests a relationship with the Pinnotheridæ through *Dissodactylus*. Hyman also describes the zoeæ of two species of *Sesarma* (*S. reticulata* and *S. cinerea*) which are very much alike. The antenna has a long and thick spinous process with very minute spines and a well-developed exopodite. The telson is forked and bears no lateral spines. Cano (1891) describes the development of *Pachygrapsus marmoratus*, the zoeæ of which resemble *Sesarma* in essentials. He shows three zoeal stages, probably first, second, and fourth or fifth, the last having lateral spines on the abdominal segments 3 to 5. The larva described by Cano as *Plagusia* he afterwards recognized as an *Ebalia* (identified above as *E. cranchii*). His larvæ of *Euchirograpsus* and *Planes* almost certainly do not belong to the Grapsidæ.

Family GECARCINIDÆ.—Moreira (1912) describes the pre-zoea of *Cardisoma guanhumi* from Brazil as the zoea. It is almost wholly terrestrial, but goes towards brackish water to hatch its eggs. The pre-zoea seems to show that the zoea has a dorsal spine, laterals and rostral spine not showing or absent, and telson forked with no external lateral spines, the antennæ like *Portunus*. Cannon (1923) obtained pre-zoeæ, described as zoeæ, from a *Cardisoma armatum* in the London Zoological Society's Gardens. It is obvious that there were pre-zoeæ which never completely turned into true zoeæ, the spines not being properly developed, but enough is seen to show that there are dorsal, rostral, and lateral spines to the carapace, and a forked telson without lateral spines. These were hatched out in sea-water and brackish water.

Family OCYPODIDÆ.—Hyman (1920) describes the life-history of three species of the American *Gelasimus*, *G. pugilator*, *G. pugnax*, and *G. minax*. These are all much alike. Five zoeal stages. Zoeæ without lateral spines to the carapace. Rostral and dorsal spines short. Antennæ with short but well-developed exopodite ending in spines; the spinous process with very short spinules along its length. Knobs on second and third abdominal segments in all stages. No long lateral spines to abdominal segments in any stage. Telson forked with no lateral spines, one pair of extra internal setæ in stages 3 to 5. Megalopa with feelers on the last joint of the last leg. No dorsal spine on carapace; rostrum apparently bent down (?). Young crab with flat front to carapace.

Oxyrhyncha. Family MAIIDÆ.—Cano (1893) describes the larvæ of *Maia verrucosa* from the Mediterranean which resembles *M. squinado* very closely. It is striking, however, that the first young crab stage has a very pronounced bicornuate rostrum which suggests a relationship with *Eurynome*, hinted at above. The rostrum of the megalopa sticks out straight instead of being bent down, so that the spine is nearly hidden. He also describes the larvæ of *Lissa*, *Herbstia*, and *Acanthonyx*, the zoea of the first with a very short rostral spine and no laterals, that of the second having all the spines of the carapace, and the third being similar to *Inachus*. All these apparently have only two zoeal stages.

Family PARTHENOPIDÆ.—Cano (1893) describes the zoeæ of *Lambrus*, which, unlike the other Oxyrhyncha, appears to have certainly more than two zoeal stages and to be more like the

Brachyrhyncha. He describes three zoeal stages, but there probably are four or five. They are more like the Cancridæ, having all the carapace spines, antennæ like *Portunus*, and only one lateral spine on the telson. If these larvæ be correctly identified and represent the Parthenopidæ, then this family does not agree with the Maiidæ in any way, and is an exception among the Oxyrhyncha. Unfortunately, the megolopa is not described.

Literature.

Bell, T. (1853.) A History of the British Stalk-Eyed Crustacea. London.

Lo Bianco, S. (1904.) Beiträge z. Kennt. d. Meeres. I. Tiefsee Fischerei der *Maia*. Jena.

Bjork, W. (1913.) "Biologisch-faunistische Untersuchungen aus dem Öresund. I. Pantopoda, Mysidacea, and Decapoda." Lunds Universitets Arsskrift. N.F. Afd. 2, Bd. ix. no. 17.

Borradaile, L. A. (1907.) "The Classification of the Decapod Crustaceans." Ann. & Mag. Nat. Hist. ser. 7, vol. xix.

Brook, S. (1884.) "On the Rate of Development of the Common Shore-Crab (*Carcinus mænas*)." Ann. & Mag. Nat. Hist. ser. 5, vol. xiv.

Du Cane, C. (1839.) "On the Metamorphoses of the Crustacea." Ann. of Nat. Hist. and Mag. of Zoology, Botany, & Geology, vol. iii.

Cannon, H. S. (1923.) "A Note on the Zoea of a Land-Crab, *Cardisoma armata*." Proc. Zool. Soc. London.

Cano, G. (1890–91.) "Sviluppo postembrionale dei Gonoplacidi." Atti della R. Accademia delle Scienze di Torino, vol. xxvi.

—— (1892 *a*.) "Sviluppo postembrionale dei Cancridi." Bull. Ent. Ital. vol. xxiii.

—— (1892 *b*.) "Sviluppo dei Portunidi, Morpologia dei Portunidi e Corystoidei." Mem. di Matematica e di fisica della Societa italiana delle Scienze (detta del 40), ser. 3 *a*, vol. viii.

—— (1892 *c*.) "Sviluppo postembrionale dei Dorippidei, Leucoridi, Corystoidei e Grapsidi." *Ibid*.

—— (1893 *a*.) "Sviluppo e morfologia degli Oxyrhynch." Mitt. Zool. Stat. Neapel, vol. x.

—— (1893 *b*.) "Dorippe, studio morfologio." Atti della R. Accademia della scienze fische e matematiche, vol. ii. ser. 29, no. 9.

Claus, C. (1876.) "Untersuchungen zur Erforschung der geneologischen Grundlage des Crustaceen-Systeme. Ein Beitrag zur Descendenzlehre." Wien.

Conn, H. W. (1884 *a*.) "The Significance of the Larval Skin of Decapods." Stud. Biol. Lab. Johns Hopkins University, vol. iii. Circular no. 32.

—— (1884 *b*.) "Evidence of a Protozoea Stage in Crab Development." *Ibid*. Circular no 28, vol. iii.

Conolly, C. J. (1923.) "The Larval Stages and Megalops of *Cancer amœnus* (Herbst)." Cont. to Canadian Biology. Studies from the Biological Stations of Canada, n. s. vol. i.

—— (1925.) "The Larval Stages and Megalops of *Rhithropanopeus harrisi* (Gould)." *Ibid*. vol. ii. part 2.

Couch, R. Q. (1813.) "On the Metamorphoses of the Decapod Crustacea." 11th Ann. Rep. Cornwall Polytechnic Society, Falmouth.

—— (1853.) "Notes on the Metamorphoses of the Common Crab (*C. pagurus*)." Penzance Nat. Hist. & Antiquarian Society. Report for 1853, 1854, 1855.

Cunningham, J. T. (1898.) "On the Early Post-larval Stages of the Common Crab (*Cancer pagurus*), and on the affinity of that species with *Atelecyclus heterodon*." Proc. Zool. Soc. London.

Faxon, W. (1878-9.) "On Some Young Stages in the Development of *Hippa*, *Porcellana*, and *Pinnixia*." Bull. Mus. Comp. Zool. Harvard, vol. v.

GARSTANG, W. (1897 *a*.) "Contribution to Marine Bionomics." Journ. Mar. Biol. Assoc. n. s. vol. iv. no. 4.

—— (1897 *b*.) "On Some Modifications of Structure subservient to Respiration in Decapod Crustacea which burrow in Sand, with some remarks on the utility of specific characters in the genus *Calappa* etc." Q. J. Mic. Sci. n. s. vol. xl.

GOODSIR, J. (1842.) "On a New Genus and on six New Species of Crustacea, with observations on the development of the egg and on the metamorphosis of *Caligus*, *Carcinus*, and *Pagurus*." Edinburgh new Philosophical Journal, vol. xxxiii.

GOURRET, P. (1884.) "Consid. sur la Faune pélagique de Golfe de Marseille." Ann. d'Hist. Nat. de Marseille, T. 2, Mem. 2.

GURNEY, R. (1903.) "The Metamorphosis of *Corystes cassivelaunus* Pennant." Q. J. Mic. Soc. vol. xlvi. n. s.

—— (1924 *a*.) "The Zoea of *Eurynome aspera*." Journ. Mar. Biol. Assoc. n. s. vol. xiii. no. 2.

—— (1924 *b*.) "Decapod Larvæ in the 'Terra Nova' Expedition." Zoology, vol. viii. (Crustacea, part ix. no. 2).

—— (1926.) "The Protozoeal Stage in Decapod Development." Ann. & Mag. Nat. Hist. ser. 9, vol. xviii. July.

—— (1927.) "Report on the Larvæ of the Crustacea." Cambridge Suez Canal Expedition. Trans. Zool. Soc. part 2, 1927.

HYMAN, O. W. (1920.) "The Development of *Gelasimus* after Hatching." J. of Morph. vol. xxxiii. no. 2.

—— (1924 *a*.) "Studies on Larvæ of Crabs of the Family Pinnotheridæ." Proc. U.S. Nat. Mus. no. 2497, vol. lxiv. art. 7.

—— (1924 *b*.) "Studies on Larvæ of Crabs of the Family Grapsidæ." *Ibid.* no. 2523, vol. lxv. art. 10

—— (1925.) "Studies on Larvæ of Crabs of the Family Xanthidæ." *Ibid.* no. 2575, vol. lxvii. art. 3.

JÖRGENSEN, O. M. (1918.) "Notes on the Development of *Carcinus mænas*." Rep. Dover Marine Laboratory, 1918.

—— (1925.) "Some Crustacean Larvæ from the Northumberland Plankton." Trans. Nat. Hist. Soc. Northumberland, Durham, and Newcastle-upon-Tyne, n. s. vol. vi. part 2.

KINAHAN, J. R. (1856–9.) "Notes on Melville's Carcinological Notes." Proc. Dublin Nat. Hist. Soc. vol. ii.

—— (1857.) "Remarks on the Zoea of *Eurynome aspera*." *Ibid.* 1857.

LEACH, W. E. (1815.) Malacostraca Podophthalmata Britannicæ. Descriptions of such British Species of the Linneau Genus *Cancer* as have their eyes elevated on foot-stalks. London.

LEBOUR, M. V. (1927.) "Studies of the Plymouth Brachyura. I. The Rearing of Crabs in Captivity, with a description of the larval stages in *Inachus dorsettensis*, *Macropodia longirostris*, and *Maia squinado*." Journ. Mar. Biol. Assoc. vol. xiv. no. 3.

—— (1928.) "Studies of the Plymouth Brachyura. II. The Larval Stages of *Ebalia* and *Pinnotheres*." Journ. Mar. Biol. Assoc. vol. xv. no. 1.

MILNE-EDWARDS, A., & BOUVIER, E. L. (1894.) "Crustacés décapodes provenant des Campagnes du Yacht 'L'Hirondelle' (1886–87–88). Première Partie. Brachyures et Anomoures." Resultats des Campagnes scientifique, Albert 1er de Monaco, fasc. vii.

MONTAGU, G. (1804.) "Descriptions of Several Marine Animals found on the South Coast of Devonshire." Trans. Linn. Soc. London, vol. vii.

MOREIRA, C. (1912.) "Embryologie du *Cardisoma guanhumi*." Mém. de la Soc. Zool. de France, vol. xxv.

PALMER, R. (1920.) "A Revision of the Genus *Portunus*, etc." Journ. Mar. Biol. Assoc. xiv. 4.

PEARSON, J. (1908.) "Memoir on *Cancer pagurus*, the Edible Crab. No. 16." Rep. for 1907 of the Lancashire Sea Fisheries Laboratory, Liverpool, and Liverpool Biol. Committee.

RUSSELL, F. S. (1904.) "The Plymouth Invertebrate Fauna." Journ. Mar. Biol. Assoc. vol. vii. no. 2.

—— (1927.) "The Vertical Distribution of Marine Macroplankton. V: The Distribution of Animals caught in the Ring-trawl in the Daytime in the Plymouth Area." *Ibid.* vol. xiv. no. 3.

SAVAGE, R. E. (1926.) "The Plankton of a Herring Ground." Min. Agric. Fish. Invest., Sect ii vol ix. no. 1.

SCHLEGEL, C. (1911.) "Sur le Développement de *Maia squinado* Latr." C. R. de l'Acad Sci. Paris, vol. cliii.

SMITH, S. J. (1873.) "The Metamorphosis of the Lobster and other Crustacea. Invertebrate Animals of Vineyard Sound." Rep. U.S. Fish Comm. for 1871 and 1872, Washington.

—— (1877–82.) "On the species of *Pinnixia* inhabiting the New England Coast, with remarks on their early stages." Trans. Connecticut Acad. Arts & Sciences. vol. iv.

SPENCE-BATE, C. (1858.) "On the Development of Decapod Crustacea." Phil. Trans. Royal Soc London.

STEPHENSON, K. (1912.) "Report on the Malacostraca collected by the 'Tjalfe' Expedition etc." Vid. Med. f. d. Malm. Foren. Bd. lxiv. Copenhagen.

THOMPSON, E V. (1829.) "Zoological Researches and Illustrations of Natural History of Imperfectly-known Animals in a series of Memoirs. III. Cork 1828–34. Memoir I. On the Metamorphosis of the Crustacea and on Zoea, exposing their singular structure and demonstrating that they are not, as has been supposed, a peculiar genus, but the larva of Crustacea."

—— (1835 *a.*). "Memoir on the Metamorphosis in *Porcellana* and *Portunus.*" Entomol. Mag vol. iii.

—— (1835 *b.*) "On the Double Metamorphosis in the Decapodous Crustacea exemplified in *Carcinus mænas* L." Phil. Trans. R Soc. London, part i.

WHELDON, W. F. R. (1889.) "Note on the Function of the Spines of the Crustacean Zoea." Journ. Mar. Biol. Assoc. n. s. vol. i. no. 2.

WILLIAMSON, H C. (1900.) "Contributions to the Life-history of the Edible Crab (*Cancer pagurus*)." 18th Ann. Rep. Fish. Board for Scotland for 1899, part 3, 1900.

—— (1903.) "On the Larval and Early Young Stages and Rate of Growth of the Shore-Crab (*Carcinus mænas*) Leach." 21st Ann. Rep. Fish. Board for Scotland for 1902, Part 3.

—— (1904.) "Contributions to the Life-histories of the Edible Crab (*Cancer pagurus*) and other Decapod Crustacea etc." 22nd Ann. Rep. Fish. Board for Scotland for 1903, part 3.

—— (1911.) "On the Larval and Later Stages of *Portunus holsatus* Fabr., *Portunus puber* L., *Portunus depurator* Leach, *Hyas araneus* (L.), etc." Fish. Scotland Sci. Invest. 1909 (1911).

—— (1915.) "Decapoden I. Teil (Larven)." Nordisches Plankton, 18th Lief., vi.

EXPLANATION OF THE PLATES.

(The figures in the plates are all drawn to three scales. Scale B is half the scale of A, and C is three times the scale of A.)

PLATE I. (Coloured.) (All to Scale A.)

Fig. 1. *Portunus puber.* First zoea. From egg.
2. *Portunus corrugatus.* " "
3. *Portunus arcuatus* " "
4. *Portunus pusillus.* " "
5. *Portunus marmoreus.* " "
6. *Portunus holsatus.* " "
7. *Portunus depurator.* " "
8. *Carcinus mænas.* " "
9. ? *Pirimela denticulata.* Fourth zoea. Plankton.
10. *Cancer pagurus.* First zoea. From egg.
11. *Thia polita.* Second zoea. Plankton.

PLATE II. (Coloured.) (All to Scale A.)

Fig. 1. *Atelecyclus septemdentatus*. First zoea. From egg.
2. *Corystes cassivelaunus*. First zoea. Plankton.
3. *Xantho incisus*. First zoea. From egg.
4. *Xantho hydrophilus*. ,, ,,
5. *Pilumnus hirtellus*. ,, ,,
6. *Gonoplax rhomboides*. First zoea. Plankton.
7. *Maia squinado*. First zoea. From egg.
8. *Eurynome aspera*. ,, ,,
9. *Hyas coarctatus* ,, ,,

PLATE III. (Coloured.) (All to Scale A.)

Fig. 1. *Pinnotheres pisum*. First zoea. From egg.
2. *Pinnotheres veterum*. First zoea. Plankton.
3. *Ebalia tuberosa*. First zoea. From egg.
4. *Ebalia cranchii*. First zoea. Plankton.
5. *Inachus dorsettensis*. First zoea. From egg.
6. *Inachus dorynchus*. ,, ,,
7. *Inachus leptocheirus*. ,, ,,
8. *Macropodia longirostris*. ,, ,,
9. *Macropodia egyptia*. ,, ,,
10. *Macropodia rostratus* ,, ,,

PLATE IV.

Fig. 1. *Portunus puber*. Second zoea. (Scale A.) From egg.
2. ,, ,, Third ,, ,, ,,
3. ,, ,, Fourth ,, ,, ,,
4. ,, ,, Fifth ,, ,, ,,
5. *Portunus pusillus*. First ,, ,, ,,
6. *Polybius henslowi*. ,, ,, ,, ,,
7. *Bathynectes longipes*. ,, ,, ,, ,,

PLATE V.

Fig. 1. *Portunus puber*. Megalopa. (Scale B.) From egg.
2. ,, ,, Carapace of megalopa. (Scale B.) From egg.
3. ,, ,, First crab stage. ,, ,,
4. ,, ,, Carapace of megalopa and first to fifth young crab stage. (Scale B.)
5. *Cancer pagurus*. First young crab stage. (Scale B.) From megalopa.

PLATE VI.

Fig. 1. *Portunus depurator*. Carapace of megalopa, and first to fifth young crab stage. (Scale B.)
2. *Portunus holsatus*. Carapace of megalopa, and first to fourth young crab stage. (Scale B.)
3. *Portunus marmoreus*. Carapace of megalopa, and first to fourth young crab stage. (Scale B.)

PLATE VII.

Fig. 1. *Portunus pusillus*. Carapace of megalopa, and first to fifth young crab stage. (Scale B.)
2. ,, *arcuatus*. Carapace of megalopa, and first to sixth young crab stage. (Scale B.)
3. *Carcinus mænas*. Carapace of megalopa, and first to eighth young crab stage. (Scale B.)
4. ,, ,, Megalopa from last zoea. (Scale B.)
5. ,, ,, First zoea. (Scale A.) From egg.
6. ? *Pirimela denticulata*. Megalopa from last zoea. (Scale B.)

PLATE VIII.

Fig. 1. *Portumnus biguttatus.* Megalopa, cast skin (collected by Mr. Gurney). (Scale B.)
2. ,, ,, Carapace of same.
3. ,, ,, First young crab from megalopa (collected by Mr. Gurney). (Scale B.)
4. ? *Pirimela denticulata.* First young crab from megalopa. (Scale B.)
5. ,, ,, Carapace of second young crab from first. (Scale B.)
6. ,, ,, Abdomen of 5.
7. *Thia polita.* Third zoea from second. (Scale A.)
8. ,, ,, Carapace of megalopa, and first and second crab stage. (Scale B.)

PLATE IX.

Fig. 1. *Atelecyclus septemdentatus.* First zoea. (Scale A.) From egg.
2. ,, ,, Second zoea. ,, ,,
3. ,, ,, Third zoea. ,, Plankton.
4. ,, ,, Fourth zoea. ,, ,,
5. ,, ,, Megalopa from last zoea. (Scale B.)
6. ,, ,, Carapace of 5.

PLATE X.

Fig. 1. *Atelecyclus septemdentatus.* Fifth zoea from plankton. (Scale A.)
2. ,, ,, Carapace of megalopa, and first and second crab. (Scale B.)
3. *Cancer pagurus.* Megalopa from last zoea. (Scale B.)
4. ,, ,, Carapace of same.
5. ,, ,, Carapace of megalopa, and first to fourth young crab stage. (Scale B.)
6. *Pilumnus hirtellus.* Megalopa from last zoea. (Scale B.)
7. ,, ,, Carapace of same.
8. ,, ,, First young crab from megalopa. (Scale B.)

PLATE XI.

Fig. 1. *Pilumnus hirtellus.* Second zoea. (Scale A.) From egg.
2. ,, ,, Third zoea. ,, ,,
3. ,, ,, Fourth zoea. ,, ,,
4. Telson of zoea of *Pilumnus hirtellus* (Scale C.)
5. *Xantho incisus.* Second zoea. (Scale A.) From egg.
6. ,, ,, Third zoea. ,, ,,
7. ,, ,, Fourth zoea. ,, ,,
8. ,, ,, Megalopa. (Scale B.) ,,
9. ,, ,, Carapace of first crab stage. (Scale B.) From egg.
10. *Gonoplax rhomboides.* Second zoea. (Scale A.) Plankton.

PLATE XII.

Fig. 1. *Gonoplax rhomboides.* Third zoea. (Scale A.) Plankton.
2. ,, ,, Fourth zoea. ,, ,,
3. ,, ,, Megalopa from last zoea. (Scale B.)
4. ,, ,, Carapace of megalopa, and first to fourth young crab stage. (Scale B.)
5. *Pinnotheres pisum.* First zoea. (Scale A.) From egg.
6. ,, ,, Rostrum of same.
7. ,, ,, ? Second zoea. (Scale A.) Plankton.
8. ,, ,, Rostrum of same.
9. ,, *veterum.* Megalopa from last zoea. (Scale B.)
10. ,, *pisum.* Abdomen of first zoea. (Scale A.)
11. ,, ,, Abdomen of last zoea. (Scale A.)

PLATE XIII.

Fig. 1. ***Pinnotheres veterum.*** Second zoea. (Scale A.) Plankton.
2. ***Corystes cassivelaunus.*** Megalopa from last zoea. (Scale B.)
3. „ „ Carapace of first young crab from megalopa. (Scale B.)
4. ***Ebalia cranchii.*** First zoea. (Scale A.) Plankton.
5. „ „ Second zoea. „ „
6. „ „ Third zoea. „ „
7. „ „ Fourth zoea. „ „
8. „ „ Megalopa from last zoea. (Scale B.)
9. „ „ Carapace of fourth zoea from behind, with rostrum from front. (Scale A.)
10. „ ***tuberosa.*** Megalopa from last zoea. (Scale B.)
11. „ „ Carapace and abdomen of first zoea from behind. (Scale A.)
12. „ „ Carapace of fourth zoea from behind. (Scale A.)
13. „ „ Rostrum of fourth zoea.

PLATE XIV.

Fig. 1. ***Ebalia tuberosa.*** First young crab from megalopa. (Scale B.)
2. ***Eurynome aspera.*** Second zoea. (Scale A.) Plankton.
3. „ „ Megalopa from last zoea. (Scale B.)
4. „ „ Carapace of same.
5. „ „ Carapace of first young crab from megalopa. (Scale B.)
6. ***Maia squinado.*** Megalopa, reared from egg. (Scale B.)
7. „ „ Carapace of megalopa, and first to third young crab stage. (Scale B.)
8. ***Hyas coarctatus.*** Second zoea from first. (Scale A.)
9. „ „ Megalopa from last zoea. (Scale B.)
10. „ „ Carapace of first young crab from megalopa. (Scale B.)
11. ***Inachus leptocheirus.*** First zoea. (Scale A.) From egg.
12. „ ***dorynchus.*** Second zoea. (Scale A.) From egg.
13. „ ***leptocheirus.*** Carapace of first young crab from megalopa. (Scale B.)

PLATE XV.

Fig. 1. ***Inachus leptocheirus.*** Second zoea reared from egg. (Scale A.)
2. „ „ Megalopa from last zoea. (Scale B.)
3. „ ***dorynchus.*** Megalopa reared from egg. (Scale B.)
4. „ ***dorsettensis.*** First young crab from megalopa, reared from egg. (Scale B.)
5. „ „ Second young crab from first. (Scale B.)
6. ***Macropodia egyptia.*** Second zoea, reared from egg. (Scale A.)
7. „ ***rostratus.*** Second zoea, reared from egg. (Scale A.)

PLATE XVI.

Fig. 1. ***Macropodia egyptia.*** Megalopa from last zoea. (Scale B.)
2. „ „ First young crab from megalopa. (Scale B.)
3. „ ***rostratus.*** Megalopa reared from egg. (Scale B.)
4. The same, side view.
5. ***Macropodia rostratus.*** First young crab from megalopa. (Scale B.)
6. Rostrum of first crab stage of ***Macropodia longirostris.***
7. „ „ „ ***M. egyptia.***
8. „ „ ***M. rostratus.*** (All Scale C.)

21. The Morphology of the Isopod Head.—Part II. The Terrestrial Isopods. By H. Gordon Jackson, D.Sc., F.Z.S., Birkbeck College, University of London.

[Received March 30, 1928: Read April 17, 1928.]

(Text-figures 1-20.)

Contents.

Page

1. Introductory 561
2. Analysis and Discussion of Results 562
3. Summary of Types of Head-structure 567
4. Descriptions of Heads of Selected Genera.
    1. *Ligia oceanica* 569
    2. *Ligidium hypnorum* 571
    3. *Trichoniscus roseus* 572
    4. *Titanethes albus* 573
    5. *Tylos latreillei* 574
    6. *Scyphax ornatus* 576
    7. *Deto bucculenta* 578
    8. *Armadilloniscus* sp. 578
    9. *Scyphoniscus waitatensis* 580
    10. *Actæcia euchroa* 580
    11. *Philoscia muscorum* 582
    12. *Arhina porcellioides* and *Alloniscus brevis* 582
    13. *Oniscus asellus* 584
    14. *Porcellionides myrmecophilus* 584
    15. *Porcellio flavocinctus* and *Cylisticus convexus* 584
    16. *Rhyscotus ortonedæ* 586
    17. *Scleropactes* sp. 586
    18. *Sphæroniscus* sp. 588
    19. *Periscyphis rufocauda* 588
    20. *Saidjahus creper* 590
    21. *Suarezia heterodoxa* 590
    22. *Microcercus anomalus* 591
    23. *Cubaris officinalis*, *Eubelum*, and *Anchicubaris* 591
    24. *Calmanesia methueni* 592
    25. *Armadillidium vulgare* 592
    26. *Platyarthrus hoffmanseggi* and *Leptotrichus panzerii* 594
5. References 595

1. *Introductory.*

In the following paper the results obtained by the author's detailed study of the head of *Ligia oceanica* (1926) have been applied to the remainder of the terrestrial Isopods. A terminology was laid down in that paper, and the general principles of structure which emerged have made it possible to give an exact description of the structural features of all types of head found in this suborder.

While phylogenetic speculations founded on the structure of the head alone have not been avoided, this paper is primarily intended as a contribution to the morphological knowledge of the subject: a discussion of the whole bearing of this work on the classification of the terrestrial Isopods would have made the scope of the paper too wide, so that aspect will be deferred to a subsequent communication.

The methods employed are the same as in the study of *Ligia* already referred to. Internal examination of heads was not always necessary, and, as a rule, sagittal section with a pair of fine scissors enabled all necessary confirmatory observations, on such points as the attachment of the anterior pharyngeal processes, to be made without elaborate dissection or maceration.

In the figures illustrating this paper no attempt has been made to represent features which have no bearing on the argument—for example mouth-parts, except the mandible, have been omitted in lateral views, the eyes have been represented conventionally without indicating the number of ocelli. setæ have been omitted, etc. In other respects they are to be taken as literal and in no way diagrammatic.

The author would like to acknowledge his debt to Dr. W. T. Calman, F.R.S., for giving him access to the material required for this work and for his unvarying helpfulness in advice and criticism; also to Miss Joyce Townend, F.Z.S., for her able assistance in the preparation of the text-figures.

2. *Analysis and Discussion of Results.*

In assessing the relative importance of the structures seen on the head of the terrestrial Isopods one naturally turns for guidance to the more primitive aquatic forms. The evidence here is, fortunately, clear and unequivocal.

The frontal line is absent in all aquatic Isopods, but the supra-antennary line is a structure of great importance and is seen (especially well in the Asellota and Valvifera) as a well-defined ridge over the sockets of the two pairs of antennæ, which is often continuous on each side with the marginal line. This ridge may dip sharply down in the midline to form a V, a feature which is preserved in some terrestrial forms. The attachment of the anterior pharyngeal processes to the inside of the dorsal surface of the "skull" is always far behind this line. At the angle where the supra-antennary and marginal lines meet, there may be formed a small projection which is the forerunner of the antennary tubercle of the terrestrial Isopods. It may be noted that in some species of *Philoscia* the antennary tubercle is obsolete and the two lines are confluent as in many aquatic Isopods.

The frontal lamina in aquatic Isopods is usually sharply defined from the rest of the face between the antennary sockets, and is not flattened on to or fused with the face in any form seen by the author. In terrestrial Isopods it is only clearly separable from the face in *Ligia*, *Ligidium*, and *Tylos*, and becomes less defined as the antennary sockets migrate outwards, as occurs in all higher forms. In such forms the clypeus becomes rolled, loses the plate-like appearance it presents in more lowly forms, and the groove separating it from the frontal lamina disappears completely or is represented by a faint line.

In aquatic Isopods the maxillipedal somite is usually very clearly marked off by deep intersomitic apodemes laterally and often by an occipital groove dorsally. The lateral grooves are seen clearly in a more or less reduced condition in all terrestrial Isopods, but the occipital groove is only seen completely uncovered in *Ligia* and *Ligidium* and, in a reduced condition, in *Scyphax*, although in *Tylos* and *Titanethes* it is only partly obliterated by the carapace fold.

From the above it can be laid down that the following characters may be looked upon as primitive:—(1) the supra-antennary line, (2) a small degree of interruption between this line and the marginal line, (3) the separation of the middle part of the frontal lamina from the face and clypeus, (4) the presence of an occipital groove.

These assumptions are confirmed in the main by the conclusions which most workers on the terrestrial Isopods have reached regarding the systematic position of the families—*e. g.*, the Ligiidæ, which have the supra-antennary line well developed, are usually assumed to lie at the base of the terrestrial Isopod stock, whereas the *Porcellio*-like forms, in which the frontal line is conspicuously developed, are usually considered to be relatively high members of the suborder.

The nearest approach to the aquatic Isopods is made by *Tylos* and *Helleria*. In these genera the conformation of head characteristic of the typical terrestrial Isopods is only dimly to be perceived, and they would be scarcely intelligible if one approached them from that aspect. Compared with the aquatic forms, it can be seen that the supra-antennal line has lost its sharp projecting shelf and become merged in the general surface of the head, the middle portion of the frontal lamina has become hypertrophied and even more distinct, and the marginal lines are discontinuous at the sides (as in *Idotea*), but the clypeus approximates more in shape to that found in the Ligiidæ, and the lateral portions of the maxillipedal somite are also of the terrestrial type. On the head-structure one must assign a lowly position to these genera.

If these considerations are applied to *Ligia oceanica*, the only form which has been exhaustively studied (1926), it is found to be specialized in so far as its frontal line is prominently displayed and its marginal line and supra-antennary line are interrupted by the antennary tubercle (although it must be noted that in some other species of *Ligia* the frontal line is much less developed), but it is decidedly primitive in respect of its other characters.

The head of *Deto* is particularly instructive viewed from this standpoint. On the general structure of the head alone there would be no hesitation in placing it as a primitive form near to *Ligidium* and *Trichoniscus*, as the supra-antennary line is well developed and continuous with the marginal line, and the clypeus and frontal lamina are clearly separable; but, although the maxillipede is primitive, the character of the mandible, maxilla, and the single penis make a close association impossible. The resemblances may then be attributed to the retention of primitive characters in both, but there can be little doubt that *Deto* has arisen from a not far distant *Trichoniscus*-like ancestor, and now lies at the base of the main stock of the Oniscidæ, leading to such forms as *Oniscus* and *Porcellio.*

The transition from the *Deto* type of head to the *Philoscia* type is not difficult, and the tendency of the supra-antennary line and marginal line to form side-flaps in some species of *Philoscia* is significant. The four-segmented antennal flagellum becomes reduced to three, the endite of the maxillipede becomes shorter and less truncate, and the separate segments of the endopodite become reduced in number; but little further modification is required. The next step upwards on this line of non-tracheate forms with triarticulate antennal flagellum should lead through *Alloniscus* to *Oniscus*, but the gulf between the heads of *Philoscia* and *Oniscus*, even when narrowed by *Alloniscus*, is a considerable one, as *Oniscus* has a most remarkable similarity to *Porcellio* with its boldly-marked frontal line and vestigial supra-antennary line.

In *Porcellionides* we probably have a form which leads from the *Deto* type to *Porcellio*, but it is much further from *Deto* than is *Philoscia* and correspondingly nearer to *Porcellio* A further segment of the antennal flagellum is dropped, and tracheæ are developed in the pleopods. On the head the frontal line is well developed, although not prominent, and the supra antennary line, although distinctly indicated in some species, is in others vestigial or absent.

Scyphax possesses a type of head which in some respects stands alone. Apart from the enormous eyes (which, like those of *Actæcia*, are evidently an adaptation for a special mode of life) and the modifications associated with them, the head is lacking in salient features. The frontal line is undeveloped, the supra-antennary line is pressed closely on to the antennary sockets and broken in the middle, the antennary tubercle is obsolete, and the clypeus, although of a simple type, is fused in the middle with the face. Just as *Deto* gives the impression of being a modified *Trichoniscus*, so this head looks like a modified *Ligia*, but, although low in the scale, it is obviously far advanced from the *Ligia* type. It might be conjectured that it represents an independent offshoot somewhere near *Deto.*

Rhyscotus is another fundamentally primitive form which has undergone striking specialization in some directions. In connection with this genus the general observation may be made, that throughout the group, concurrently with specialization in other parts, the segments of the antennal flagellum tend to become reduced.

It is of importance to note that as the supra-antennary line is reduced in non conglobating forms, it is driven lower on the face till it rests on the top of the antennary sockets and restricts very considerably the area of the post-frons (*Paraphiloscia*). In the conglobating forms the reverse process seems to take place, and the line is driven high on the face till it skirts the top of the great frontal shield (*Armadillidium*).

In the former case a fold of chitin carrying the line may obscure the upper boundary of the antennary socket, and at the outer side of the socket an apparent notch is produced by the separation of the supra-antennary line from the socket. This is well seen in *Paraphiloscia gracilis*, which retains the middle portion of the line, and in many *Porcellio* species which have otherwise lost the line. In *Armadillidium vulgare* an intermediate stage can be seen where the line is partly lifted above the socket. Such a notch is best seen in forms in which the supra-antennary line is (or was) low on the face, and less frequently in those in which it is lifted high above the sockets, so that a notch in a form which has no other trace of a supra-antennary line may usually be accepted as evidence of its former existence low down on the face.

There can never be any doubt as to the identity of this line, owing to the fact that the anterior pharyngeal processes of the alar plate are always attached well behind it, and that its relations at each side with the marginal line and antennary tubercle are most characteristic. The anterior pharyngeal processes are always attached to the cranium either on or immediately behind the frontal line when this is present.

Another line of study is afforded by the genera which exhibit the power of rolling up (or "conglobation" as Budde-Lund calls it). Among the most important genera which conglobate are *Actæcia*, *Cubaris*, *Periscyphis*, *Microcercus*, *Saidjahus*, *Suarezia*, *Scleropactes*, *Eubelum*, *Toradjia*, and *Armadillidium*.

In all these forms the head tends to become flattened in an antero-posterior direction. Where the faculty is highly developed the upper surface (vertex-occiput) and the genæ become narrow strips, the face becomes flattened and vertical, and the middle part of the frontal lamina and clypeus and the post-frontal area with the supra-antennary line are driven high up on it. The antennary sockets are often protuberant. The distribution of the origin of the adductor mandibularis is little indication of the boundary between frontal area and vertex, as the restricted upper area of the head may cause part of the origin of the muscle to be placed on the face below the frontal line. The anterior pharyngeal processes, however, remain attached to the frontal line, so that they may lie partly within the mandibularis muscle.

The same general type is common to all, but it is most improbable that all these types are nearly related and that conglobation has only arisen once in the terrestrial Isopods. The *Cubaris* and *Armadillidium* types have much in common, the differences being expressed in other parts of the body than the head—especially in the uropoda, which have become specialised in opposite directions.

There are several conglobating forms, such as *Periscyphis*, *Saidjahus*, and *Suarezia*, which are related to the *Cubaris*-type and which show varying degrees of specialisation in head and body, and in all these the supra-antennary line seems to have been forced up high on the face.

Scleropactes is an interesting form, as it shows the supra-antennary line in process of reduction and the uropods in a condition approaching that of *Cubaris*, but the supra-antennary line is low on the face and immediately above the antennary sockets, the antennary tubercle is low down, and the clypeus is of a comparatively simple type. This is no doubt one of the more primitive rolling types, and the truncate endite of the maxillipede and the triarticulated antennal flagellum also point in this direction. On the other hand, tracheæ are said to be present in the pleopods. The exaggerated frontal shield characteristic of conglobating forms is well shown, in contrast, as it were, to the rest of the otherwise lowly head. The temptation, on the evidence of the head, to put this form low down in a line leading through *Suarezia*, *Saidjahus*, and *Periscyphis* (with secondary reduction of the frontal line) to *Cubaris* is modified by our present knowledge of the geographical distribution of these forms. On the evidence of the head one can equally well argue that the *Periscyphis*-group has never had a frontal line and is in process of gaining one, so that its highest form would be *P. latissimus* with the complete frontal line (and vestigial exopod to the uropod). The complete absence of supra-antennary line postulates, however, a high position in the series for this genus.

Actæcia, which by its general anatomy must be classified as one of the more primitive forms, shows in the head a specialisation for rolling as extreme as that of *Cubaris* and in some respects resembling it. The retention of distinct portions of the middle part of the frontal lamina is an unusual feature, but this structure and the middle part of the clypeus have migrated far up on the face. One can only conclude that *Actæcia* has become quite independently modified in the same direction as the higher conglobating forms.

Eubelum differs so little in head-structure from *Cubaris* as to require no separate consideration, but it is improbable that these genera are as nearly related as that would seem to imply, when other structural featues are taken into account.

The author has seen none of the original specimens of *Toradjia* described by Dollfus, and has doubts about the correct identification of the specimens so named by Budde-Lund; but from the figures and descriptions available, it is not clear whether the middle of the frontal line has been drawn backwards over the vertex, or whether a tongue formed from the frontal shield has been drawn over the frontal line and applied to the upper surface of the head. If the greatly elevated median carina of *Armadillidium nasatum* were flattened on to the upper surface of the head, such an effect could be produced.

The form of the *clypeus* in the terrestrial Isopods is progressively modified throughout the group and is of some interest. In *Ligia* and related forms it is almost flat and applied as a shield to the face, and is in the same plane as the labrum. A deep groove separates it from the face in *Tylos*, *Ligia*, *Trichoniscus*, and *Ligidium*, and to a less extent in *Titanethes*. In the remaining forms it is never expanded or separated from the face by anything more than a shallow depression. It arises from the face at an angle approximating to a right angle and bends sharply down to connect with the labrum. There is therefore a horizontal ledge or shelf formed between the antennary sockets. (In the following descriptions this condition is termed "set off from face.") The distal portion of the clypeus is turned over to become more or less in the same plane as the labrum (*Armadillidium*, *Philoscia*, *Porcellio*), but the distal edge may itself be sharply returned so that this portion of the clypeus forms a projecting roll in the form of an ogee (*Cubaris*). In conglobating forms the antennal sockets tend to be forced far apart, and the clypeus becomes narrow and lifted between them, the lateral processes sometimes becoming deformed and folded (*Cubaris*, *Armadillidium*, *Periscyphis*). The anterior apophysis of the mandible articulates with the clypeus between its body and its lateral processes.

3. *Summary of Types of Head-structure.*

The types of head found in the terrestrial Isopods can be classified broadly under the following sections:—

A. Tylos-type. (Text-fig. 6 (A) & (B).)

Flattened from above downward, vertex and profrons being in one plane so that the supra-antennary line forms the anterior margin of the top of the head. Middle part of frontal lamina massive and well defined from face. Clypeus wide and deep, but with very small lateral processes. Occipital groove on hind border of head. Antennary sockets close together. Attachment of anterior pharyngeal processes far back on dorsal surface of head. Antennary tubercle not clearly differentiated. (*Tylos*, *Helleria*.)

B. LIGIDIUM-type. (Text-figs. 1–9, 11, & 12.)

Includes heads retaining many primitive features. The profrons is no longer in the same plane as the vertex, but is usually raised to approximate to the plane of the postfrons, thus forming a distinct "face" and "forehead." Supra-antennary line very distinct, and usually closely associated with marginal line in the neighbourhood of the antennary tubercle. Clypeus more or less flattened, and often separated from frontal lamina by a distinct crease.

This section divides itself into three groups which tend to overlap:—

1. In which the occipital groove is uncovered; the middle part of the frontal lamina is distinct and the clypeus flat and clearly defined from the frontal lamina: the "forehead" is raised so that the face approaches the vertical; antennal sockets close together. (*Ligidium*, *Ligia* and possibly *Scyphax*, although this form does not quite square with the definition.)

2. In which the occipital groove is covered by a carapace fold; the middle portion of the frontal lamina is fused with the face; the clypeus is not clearly defined from the frontal lamina, but remains flat and "*Ligidium*-like"; the head is compressed dorsoventrally so that the "forehead" is receding and the clypeus and labrum sloped forward to give, in side view, a prognathous appearance; antennal sockets further apart than in preceding group. (*Trichoniscus*, *Titanethes*, *Deto*, *Armadilloniscus*, *Scyphoniscus*.)

3. In which the characters are as in Group 2, but the clypeus is set off from the face and no longer flattened, the "forehead" is raised and the "face" approaching the vertical, and the antennary sockets have further diverged. (*Philoscia*, s. lat., *Alloniscus*, and related genera.)

C. PORCELLIO-type. (Text-figs. 13 & 14.)

Frontal line strongly developed or secondarily reduced (*Hemilepistus*), often forming prominent lobes. Supra-antennary line vestigial or only feebly represented, pro- and postfrons being usually confluent. Marginal line usually well defined under eyes and passing downwards uninterruptedly to lower margin of cheek. Clypeus set off from face. Head not flattened dorsoventrally, but never shortened in an antero-posterior direction like the next section. (*Porcellio*, s. lat., *Oniscus*, and related genera.)

D. CUBARIS-type. (Text-figs. 17–19.)

This section is unnatural, as it includes the conglobating types, which all conform more or less to the same plan, but may not on that account be related.

Frontal line usually strong and raised into crest, which forms upper edge of more or less flat frontal shield. Supra-antennal line vestigial or only feebly represented. Antennary tubercle usually high on face and sometimes raised into distinct ridge. Clypeus set off from face, often rolled and raised between antennary sockets. Head compressed antero-posteriorly so that its height greatly exceeds its depth. (*Cubaris*, *Spherillo*, *Armadillidium*, *Periscyphis*, *Microniscus*, and related forms.)

Scleropactes and *Actæcia* stand in separate categories, as has been explained above.

4. *Descriptions of Heads of Selected Genera.*

Below are given uniform descriptions of the heads of every genus of terrestrial Isopod available to the author which seemed to differ sufficiently from their fellows to merit it. The species chosen for description was that of which the best specimens were obtainable and which seemed best to illustrate the general structure in the genus. Each generic description may be looked upon as a central point which will illuminate the structure of any nearly related genus or subgenus, and thus cover more or less completely the whole field.

The description of *Ligia oceanica* which subjoins is drawn up on the same plan as the others for the sake of uniformity, and illustrated by the same figures as in a previous paper on the subject (1926).

1. LIGIA OCEANICA (Linn.). (Text-figs. 1 & 2.)

Clypeus: smooth, flat, and large, separated by deep fissure from frontal lamina; lateral processes small and pressed back.

Frontal lamina: antennal socket large, well defined, and close together; lower and middle part of lamina well marked; median projection fused with face.

Antennary tubercle: blunt and flat but well marked, lying high on side of face; marginal and supra-antennal lines lie close together upon it.

Postfrons: large and well marked off by strongly-developed supra-antennal line, which forms a V in mid-line.

Profrons: a large area well marked off by frontal line, which curves down to end on each side beneath eyes.

Vertex: with well-marked interocular line and shallow postocular pits.

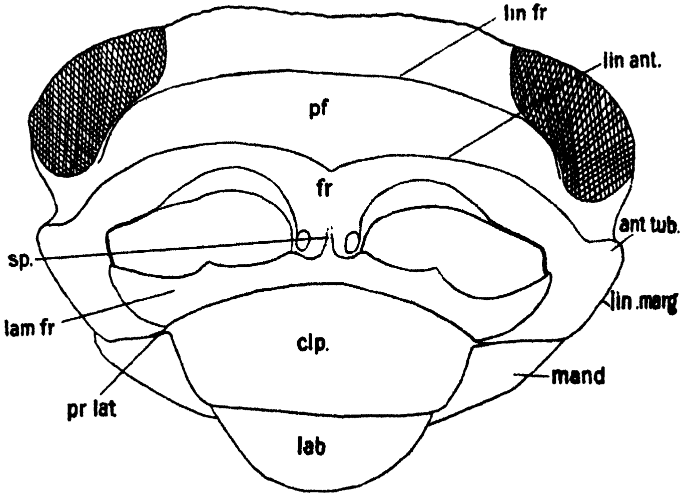
Occipital groove: passes across dorsal surface, cutting off the maxillipedal somite from the rest of the head.

Marginal line: well marked throughout, forming front border of occipital groove and passing over antennary tubercle.

Gena: large and high; deep genal fossa and distinct genal groove.

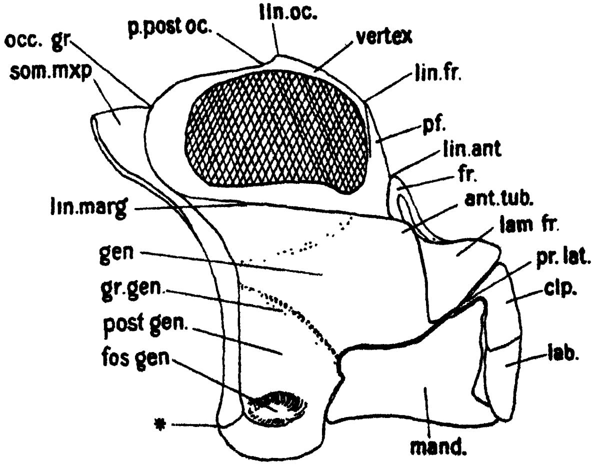
Remarks: all primitive features are well marked in this head,

Text-figure 1.



Outline of head of *Ligia oceanica* seen from the front †.

Text-figure 2.



Outline of head of *Ligia oceanica* seen from the side †.

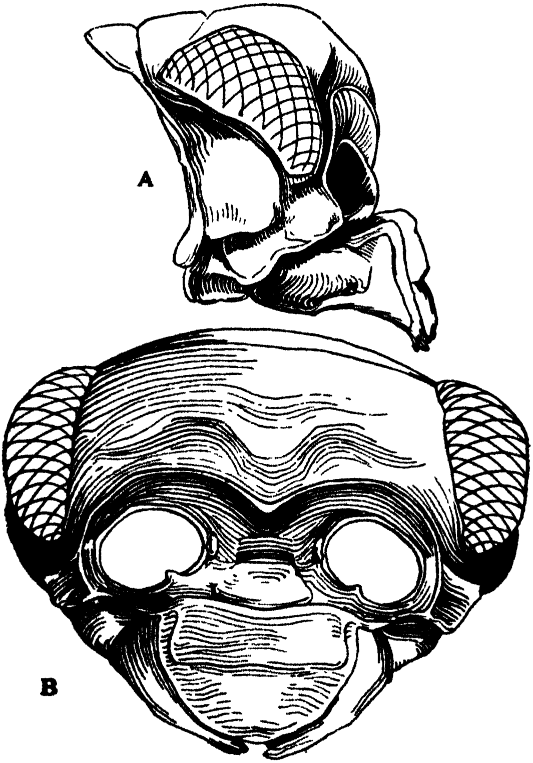
† Key to text-figs. 1 and 2:—*ant.tub.*, antennary tubercle; *clp.*, clypeus; *fos.gen.*, genal fossa; *fr.*, postfrons; *gen.*, gena; *gr.gen.*, genal groove; *lab.*, labrum; *lam.fr.*, frontal lamina; *lin.ant.*, supra-antennal line; *lin.fr.*, frontal line; *lin.marg.*, marginal line; *lin.oc.*, interocular line; *mand.*, mandible; *occ.gr.*, occipital groove; *p.postoc.*, postocular pit; *pf.*, postfrons; *postgen.*, postgena; *pr.lat.*, lateral process of clypeus; *som.mxp.*, maxillipedal somite; *sp.*, median spine of frontal lamina; *, fissure between maxillipedal somite and cephalon where occipital groove passes to ventral surface of head.

combined with more specialised characters which attain a more elaborate development in higher groups.

2. LIGIDIUM HYPNORUM (Cuv.). (Text-fig. 3.)

Clypeus: similar to that of *Ligia*, flattened, very small lateral processes; upper edge raised and folded against frontal lamina, but less so than in *Ligia*.

Text-figure 3.



Ligidium hypnorum **viewed (A) from the side, (B) from the front.**

Frontal lamina: middle part proportionately wider than in *Ligia*, the distance between antennal sockets being greater; lower edge very distinctly marked off, upper fused with face; antennal sockets closely applied to face.

Antennary tubercle: obsolete.

Postfrons: similar to that of *Ligia*; supra-antennal line well defined, passing downward on either side of antennæ and then sharply backwards nearly to join marginal line; well-marked V in mid-line.

Profrons: confluent with vertex, as frontal line is absent; the curvature of the "forehead," however, marks its position and indicates a similar course to that of *Ligia*.

Vertex: interocular line indistinct; shallow postocular pits.

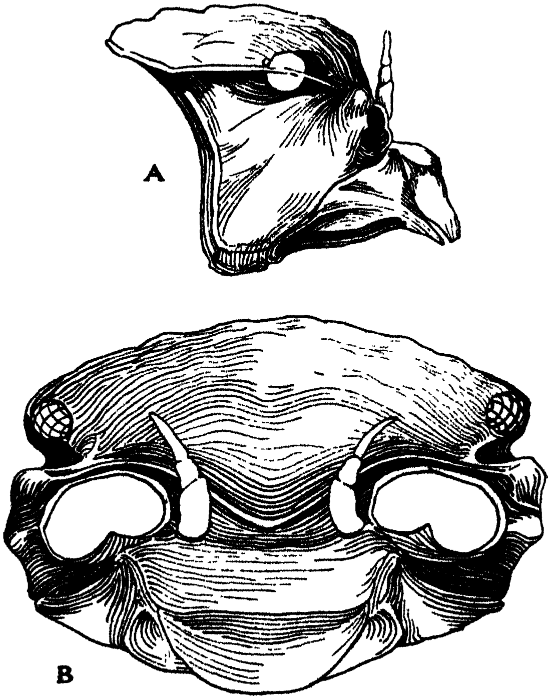
Occipital groove: strongly developed and deeper dorsally than in *Ligia*.

Marginal line: well marked and continuous throughout.

Gena: very smooth and little excavated beneath eyes; no genal groove; genal fossa well marked.

Remarks: the frontal lamina is in an interesting intermediate stage of reduction; a head which rather suggests that it has lost the more specialised characters of *Ligia* than of being more primitive than it.

Text-figure 4.



Trichoniscus roseus viewed (A) from the side, (B) from the front.

3. Trichoniscus roseus (Koch). (Text-fig. 4.)

Clypeus: similar to *Ligia*, a deep groove between it and frontal lamina; lateral processes very small.

Frontal lamina: middle part fused with face, although an ill-defined groove may mark line of fusion; antennal sockets very laterally placed so that they press on antennary tubercle; closely applied to face.

Antennary tubercle: high on side of face and prominent; supra-antennal line runs on it and nearly meets marginal line, which curves forward from beside eyes.

Postfrons: restricted by median downward sweep of supra-antennal line, which is strongly marked.

Profrons: confluent with vertex, but distinctly separable from it by absence of tubercles; frontal line an ill-defined shallow groove between eyes, difficult to make out without exposure of anterior pharyngeal processes in sagittal section.

Marginal line: forms hind border of head; well defined laterally and raised so as to pass across eyes; becomes obscure on reaching antennary tubercle.

Gena: slightly concave under eyes; no genal groove or fossa.

Remarks: this head has undergone the opposite process to the conglobating forms (*Cubaris* etc.). The vertex has passed forwards, encroached on the frontal area and bent the supra-antennal line down, whereas in *Cubaris* the frontal area has expanded greatly upwards, pushing the vertex back and making the top of the head very narrow. Whole head markedly flattened. but related to *Ligia*. The occipital groove has disappeared.

4. TITANETHES ALBUS (Koch). (Text-fig. 5.)

Clypeus: smooth, flat, and large, shaped like *Ligia*, but tilted upwards so as to protrude sharply from face; lateral processes small and pressed back.

Frontal lamina: middle part obscured by clypeus, which projects upwards and forms a deep groove between it and frontal lamina as in *Ligia*; antennal sockets well defined, slightly overhung at sides by supra-antennal line.

Antennary tubercle: prominent lobes on each side of and slightly above antennal sockets; supra-antennal line terminates on tubercle.

Postfrons: small area restricted by low-curving supra-antennal lines; slightly bulbous.

Profrons: confluent with vertex, but distinguishable from it by absence of tubercles.

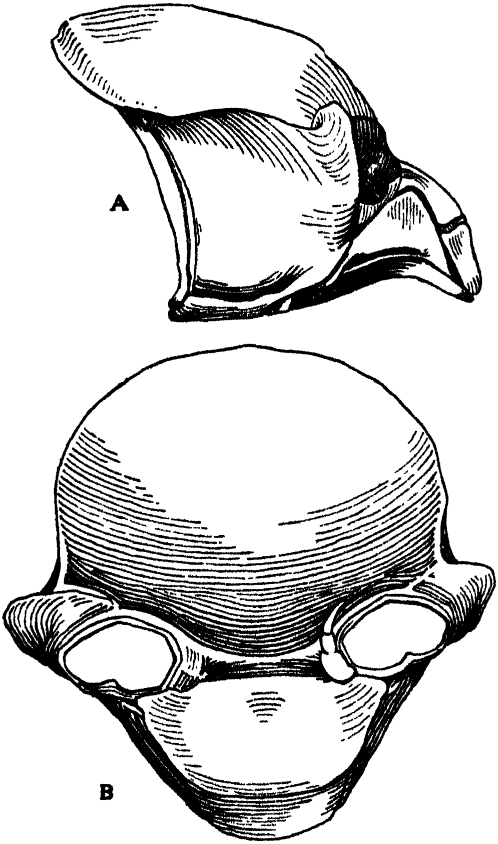
Occipital groove: upon hind margin of head facing backwards.

Marginal line: forms hind margin of head coequal with posterior edge of occipital groove; distinct laterally and ending on antennary tubercle.

Gena: flat, only slightly excavated; no genal groove or well-marked genal fossa.

Remarks: a similar head to the preceding, but recalling *Deto* in its general form.

Text-figure 5.



Titanethes albus viewed (A) from the side, (B) from the front.

5. Tylos latreillei Aud. (Text-fig. 6.)

Clypeus: massive and tuberculated, upper edge projected forward to form thick roll; wide, but without large lateral processes.

Frontal lamina: middle portion in form of triangular projecting shield, fused with face above, although easily separable; lower edge separated from clypeus by deep cleft; antennal sockets well marked below, but difficult to separate from face above.

Antennary tubercle: a structure at each side of antennal socket appears to consist of supra-antennal line, marginal line, and antennary tubercle, but the structure is not distinctly developed.

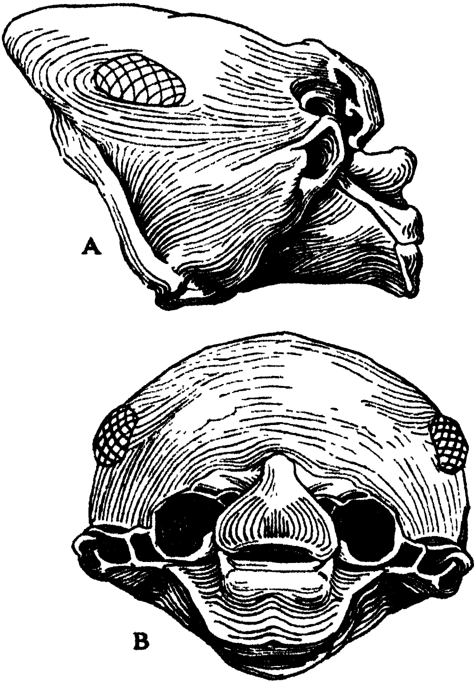
Postfrons: ill defined; supra-antennal line distinguishable over sockets, but somewhat feeble between them.

Profrons: confluent with vertex; well-marked attachments of anterior pharyngeal processes between eyes show anterior margin of vertex, but frontal line is entirely absent.

Occipital groove: upon hind margin of head facing backwards.

Marginal line: defines posterior margin of head, coequal with posterior edge of occipital groove; scarcely distinguishable laterally.

Text-figure 6



Tylos latreillei viewed (A) from the side, (B) from the front.

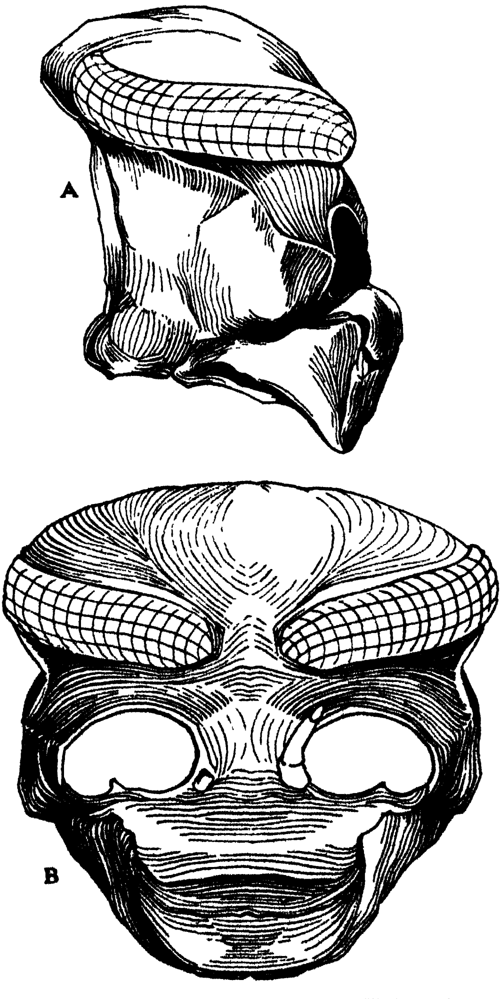
Gena: smooth, concave; genal fossa scarcely formed.

Remarks: the head has a strong general resemblance to *Idotea*, especially in the facial region, the disposition of frontal lamina, sockets and supra-antennal lines being especially similar. The other characters are on the whole terrestrial, although it would appear never to have possessed a frontal line.

6. **Scyphax ornatus** Dana. (Text-fig. 7.)

Clypeus : smoothly convex, not separable from face in mid-line; lateral processes moderately large.

Text-figure 7.



Scyphax ornatus viewed (A) from the side, (B) from the front.

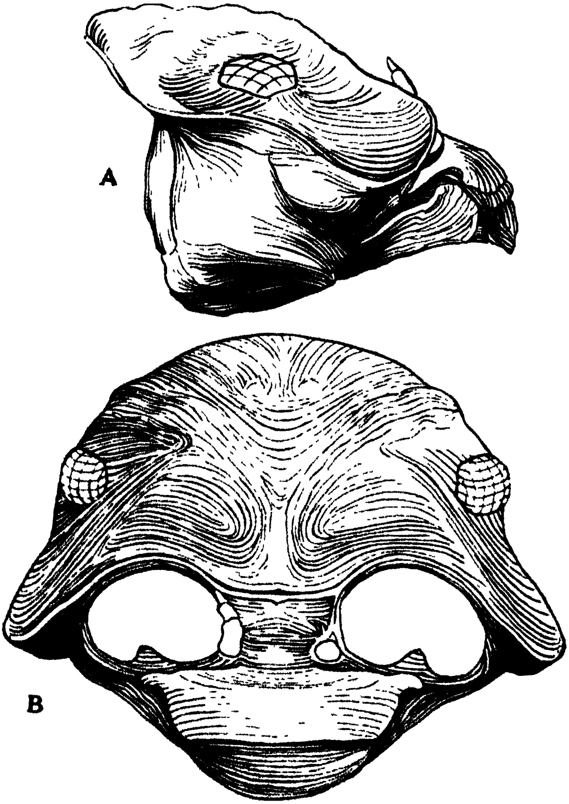
Frontal lamina : middle portion obsolete; lower portion of antennal sockets feebly defined, upper part masked by heavy fold from postfrons carrying supra-antennal line.

Antennary tubercle: not obvious, but may be represented by a knob at each side of head below marginal line.

Postfrons: not clearly defined from profrons; supra-antennal line passes over antennary sockets and runs sharply downwards between them to inner side of antennules, where it becomes lost.

Profrons: confluent with vertex; frontal line absent, but from position of anterior pharyngeal processes the profrons may be assumed to end above and between the eyes, which have encroached upon it.

Text-figure 8.



Deto bucculenta viewed (A) from the side, (B) from the front.

Occipital groove: obliterated dorsally, but from the marginal line and other indications it is obviously morphologically in the same position as in *Ligia*.

Marginal line: very well defined laterally, turns forward in front and ends at side of supra-antennal line, just lateral to antennal sockets; at hind margin of eye it turns upwards and disappears on dorsal surface; hind margin of head formed by maxillipedal somite.

Gena: slightly concave; genal fossa shallow.

Remarks: must be classed as a primitive head, with individual modifications.

7. DETO BUCCULENTA. (Text-fig. 8.)

Clypeus: upper part calcified, lower membranous; defined from face by slight groove; lateral processes moderately large: labrum and clypeus resembling *Ligia*, but protruded forwards so that the face forms a wide angle with the "foramen magnum."

Frontal lamina: middle part fused with postfrons, from which it is only separated by a shallow depression; antennal sockets moderately defined and very overshadowed by supra-antennal line and antennary tubercles, which bulge over them.

Antennary tubercle: drawn outwards and forwards to form a pair of lobes simulating lateral lobes (formed from frontal line in *Porcellio* and *Oniscus*); supra-antennal line runs round its edge and meets marginal line.

Postfrons: restricted in area by low-curving supra-antennal line which runs closely over antennal sockets.

Profrons: confluent with vertex, as frontal line is absent.

Marginal line: distinct, but feeble laterally; passes under carapace fold at hind border; in front becomes confluent with supra-antennal line.

Gena: flat, only slightly concave; very broad and low; no genal fossæ.

Remarks: this head has a superficial resemblance to *Oniscus* and *Porcellio*, but really is widely removed. The antennary tubercles have, in fact, been mistaken for lateral lobes. It has most in common with *Trichoniscus*, both retaining many primitive features as well as the general shape, large antennary tubercles, and low-curving supra-antennal line.

8. ARMADILLONISCUS sp. (Text-fig. 9.)

Clypeus: scarcely defined from face; lateral processes large; protruded forwards and generally similar to *Deto*, but approaching nearer to the higher forms.

Frontal lamina: middle part not at all defined; antennary sockets well defined, very large and placed low down.

Antennary tubercle: prominent lobes similar to those of *Deto* and similarly bulging over antennal sockets; probably carrying supra-antennal line, which, however, is less distinctly joined on than in *Deto*.

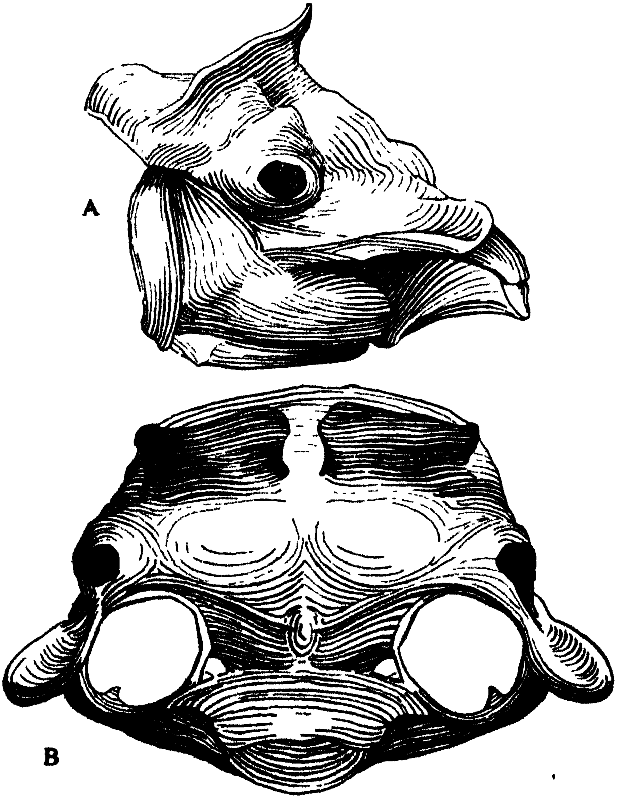
Postfrons: small area defined above by rather weak supra-antennal line, which is obsolete in mid-line, where it is interrupted by a tubercle; passes over antennal sockets to antennary tubercle.

Profrons: confluent with vertex, as frontal line is absent.

Vertex: in this species bears a pair of flat, transverse, vertical plates which have no morphological significance.

Marginal line: forms hind margin of head, passes forward under eyes, and becomes lost on antennal tubercle.

Text-figure 9.



Armadilloniscus sp. viewed (A) from the side, (B) from the front.

Gena: very broad and low; maxillipedal somite wide laterally; no genal groove or fossa.

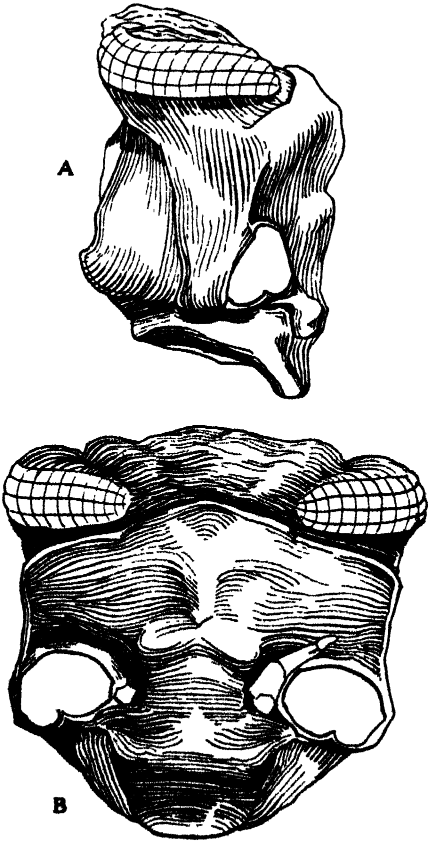
Remarks: this head has many characters in common with *Deto*; the supra-antennal line, though less defined, has similar relations with antennary tubercles; the face is extremely protuberant and long. The specimen here described is from Budde-Lund's collection (British Museum), and is there labelled

"*A. bilobatus* B.-L.," but no description of it seems to have been published.

9. SCYPHONISCUS WAITATENSIS Chilton.

This genus does not require a separate description from *Armadilloniscus*, as the general type is very similar. The antennary lobes are less pronounced than in that genus and the supra-antennal line is absent.

Text figure 10.



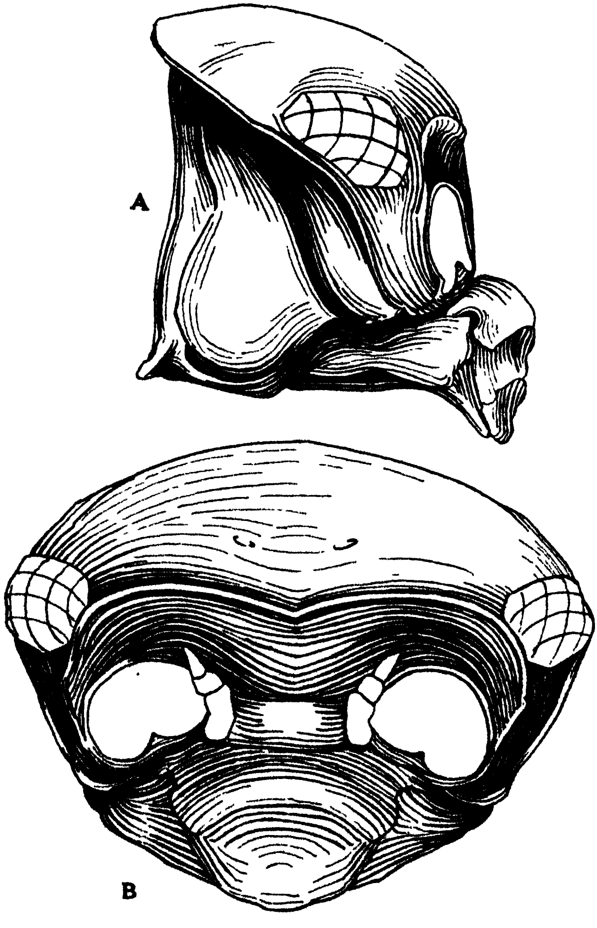
Actæcia euchroa viewed (A) from the side, (B) from the front.

10. ACTÆCIA EUCHROA Dana. (Text-fig. 10.)

Clypeus: drawn up high in mid-line and only doubtfully separable from frontal lamina; body lobed on each side, lower part membranous; lateral processes moderately large and drawn out very fine.

Frontal lamina: drawn up high on to face in mid-line, where it is probably represented by a pair of convex protuberances; antennal sockets moderately defined below, overshadowed above and at sides by vestigial fold of supra-antennal line.

Text-figure 11.



Philoscia muscorum viewed (A) from the side, (B) from the front.

Antennary tubercle: not patent.

Postfrons: not clearly delimited; antennular sockets low down by antennal sockets; no supra-antennal line other than the vestigial fold referred to; the median V-shaped ridge may represent a part of it.

Profrons: bounded above by raised frontal line, forming a high shield extending laterally to sides of antennal sockets.

Marginal line: ill defined laterally; passes under hind border of head, which is produced far back so as markedly to overlap and obliterate the maxillipedal somite, a modification probably due to the enormous development of the eyes.

Gena: posterior edge reflected so that a portion of the gena faces backwards; genal groove deep; genal fossa absent.

Remarks: a head modified in the same direction as the other conglobating genera, but remarkably different in detail and obviously entirely unrelated to them.

11. PHILOSCIA MUSCORUM (Scop.). (Text-fig. 11.)

Clypeus: set off from face and gently rolled; separated by distinct groove from face; lateral processes small.

Frontal lamina: middle part bulbous, distinctly separated by groove from frontal area; antennal sockets defined and flat on face.

Antennary tubercle: very reduced and low down.

Postfrons: slightly bulbous; a large area similar in extent to that of *Ligia* and *Ligidium*; supra-antennal line very well developed, curving down on each side to pass over outer edge of antennal sockets; sinuate in mid-line; ends on antennary tubercle without attaining marginal line in this species.

Profrons: confluent with vertex, as frontal line is absent.

Marginal line: forms hind margin of head; very distinct and well marked throughout.

Gena: slightly concave; genal groove present; genal fossa shallow.

Remarks: in some "*Philoscia*" the supra-antennal line and marginal line meet on the antennary tubercle as in *Deto* and other primitive forms. The head is an interesting illustration of a movement from the *Ligidium*-type towards the higher members of the suborder.

12. ARHINA PORCELLOIDES B.-L. (Text-fig. 12.)

Clypeus: set off from face; distinctly separated by shallow groove; lateral processes moderately large and grooved off from body of clypeus.

Frontal lamina: middle portion ill defined, but a short shallow median groove may mark its separation from postfrons; antennal sockets well-defined below, obscured above by supra-antennal line.

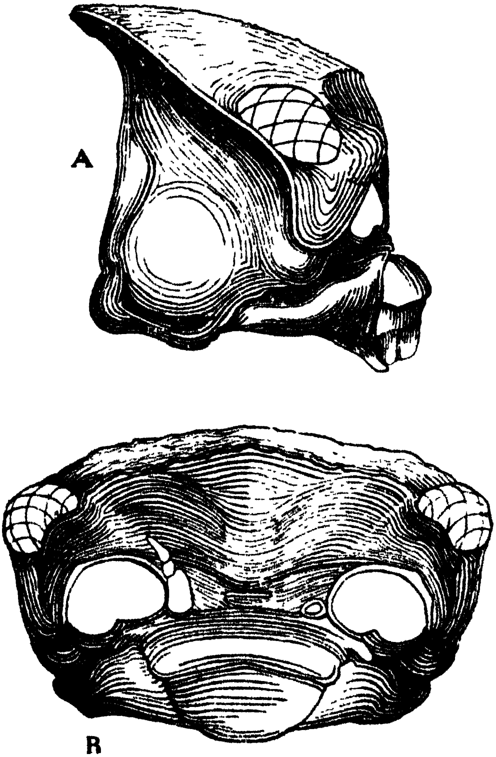
Antennary tubercle: very reduced and low.

Postfrons: narrow from above downwards and sharply separated from profrons by well-defined supra-antennal line, which passes over antennal sockets and joins marginal line at side of face just above antennary tubercle.

Profrons: separated from vertex by very distinct margin, which is studded with small tubercles, but hardly forms distinct and continuous frontal line; in front and slightly to inner side of eye is ill-defined frontal lobe, on which this rudimentary line ends.

Marginal line: forms hind border of head; sharply-defined laterally, passes downward in front of eye and joins supra-antennal line.

Text-figure 12.



Arhina porcelloides viewed (A) from the side, (B) from the front.

Gena: smooth; no genal groove; genal fossa deep.

Remarks: a further forward progression from *Philoscia*. A genus related to *Alloniscus*, which greatly resembles it. *Alloniscus brevis* B.-L. differs only in the very bulbous postfrons, and the supra-antennal line is not continuous with the marginal line at the side of the antennal socket.

13. **Oniscus asellus** Linn.

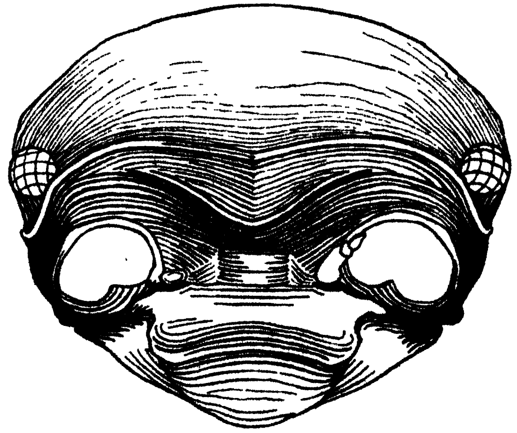
In all but points of minute detail the description and figures given below of *Porcellio flavocinctus* applies equally well to this genus.

14. **Porcellionides myrmecophilus** (Stein). (Text-fig. 13.)

Clypeus: set off from face and rolled; fused indistinguishably with frontal lamina above; lateral processes rather small.

Frontal lamina: middle portion obsolete, but probably defined in mid-line by short deep groove; antennal sockets moderately well defined.

Text-figure 13.



Porcellionides myrmecophilus viewed from the front.

Antennary tubercle: vestigial and low down.

Postfrons: partially separated by a median V, evidently part of supra-antennal line, from profrons; supra-antennal line otherwise incomplete and in some species absent.

Profrons: defined above by strongly-developed frontal line, which is produced in front of eyes into weak lateral lobes.

Marginal line: forms hind border of head; well marked and continuous laterally.

Gena: genal groove well marked; genal fossa present.

Remarks: an interesting stage in the reduction of the supra-antennal line and development of frontal lateral lobes, approaching *Porcellio*.

15. **Porcellio flavocinctus** B.-L. (Text-fig. 14.)

Clypeus: set off from face and rolled; upper margin defined by slight groove; lateral processes large.

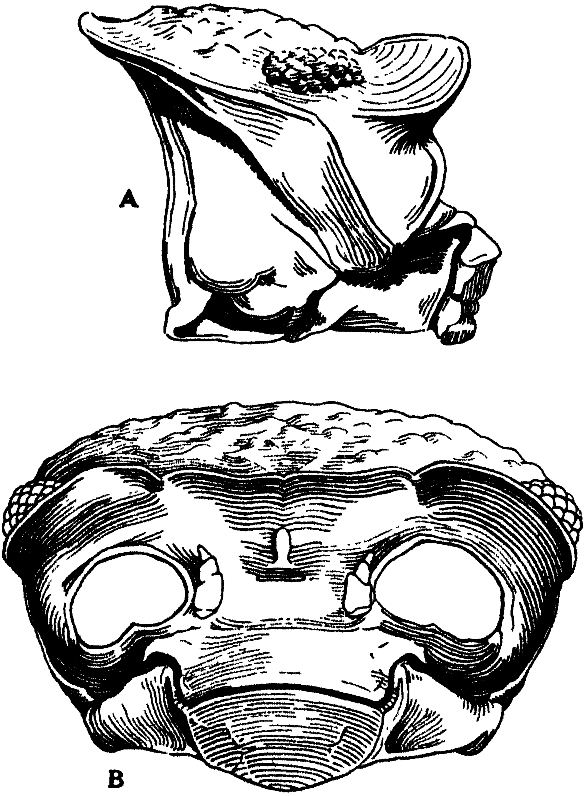
Frontal lamina; middle portion indistinctly defined, and with median slot-like groove; antennal sockets well defined, but flat on face; fused above with vestigial supra-antennal line.

Antennary tubercle: nearly obsolete and low down.

Postfrons: not separate from profrons, the middle portion of the supra-antennal line being absent.

Profrons: limited above by frontal line, which forms prominent crest; frontal line drawn out in front of eyes to form prominent rounded frontal lobes.

Text-figure 14.



Porcellio flavocinctus viewed (A) from the side, (B) from the front.

Marginal line: forms posterior margin of head; very distinct laterally, passes downwards in front of eyes and becomes lost on antennary tubercle.

Gena: deeply concave; genal groove; fossa well developed.

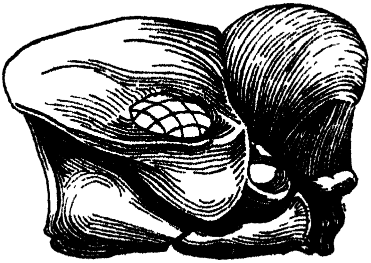
Remarks: the most highly-developed head of the non-conglobating type. *Cylisticus convexus* (de Geer) differs in no important respect from *Porcellio scaber*, and shows no modification whatever for conglobation. *Bathytropa* is also of the *Porcellio*-type.

16. Rhyscotus ortonedæ B.-L. (Text-fig. 15.)

Clypeus: forms a narrow rib continuous at each side with lateral processes, which are turned up to run on inner side of antennal socket; middle portion may be extended upwards on to frontal lamina, but is not recognizable; owing to peculiar position of lateral process, anterior apophysis of mandible is directed upwards in order to articulate with it.

Frontal lamina: antennal sockets thrown to each side by enormously hypertrophied middle portion, which forms tumour-like structure.

Text-figure 15.



Rhyscotus ortonedæ viewed from the side.

Antennary tubercle: obsolete.

Postfrons: defined above by well-marked supra-antennal line, but its area is encroached on and almost obliterated by bulbous frontal lamina.

Profrons: confluent with vertex as frontal line is absent.

Marginal line: forms posterior margin of head; distinct laterally as far as eyes, under which it becomes lost.

Gena: very broad and low owing to flattening of whole head.

Remarks: a head possessing remarkably specialized features, grafted on to a fundamentally primitive structure.

17. Scleropactes sp. (Text-fig. 16.)

Clypeus: little set off from face, only slightly rolled; indistinctly separable from face; lateral processes moderately large and pressed back.

Frontal lamina: middle portion obsolete; antennal sockets very well defined, fused above with supra-antennal line, which, however, does not form obscuring fold.

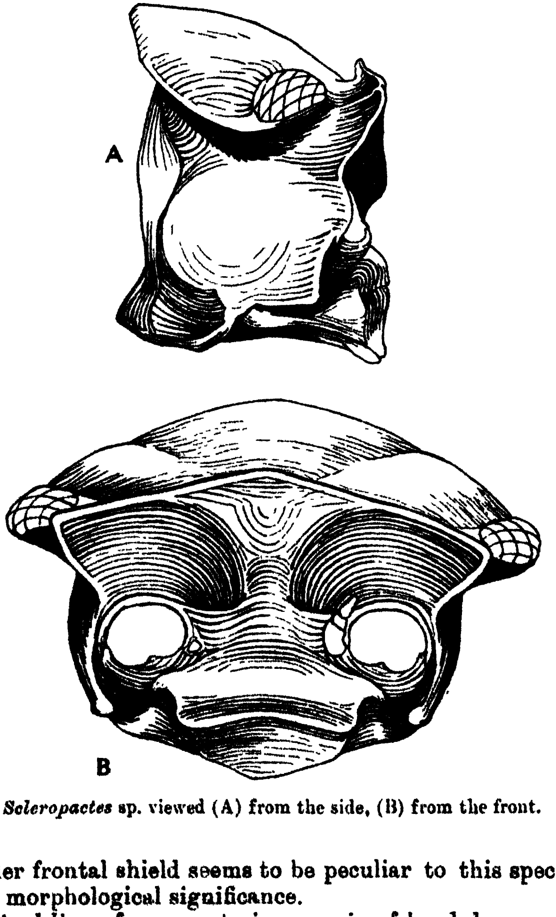
Antennary tubercle: not distinctly developed, although it may be represented by slight fold at each side of head, below and to the side of the antennal sockets.

Postfrons: distinctly demarcated by weak supra-antennal line, which is produced from above antennal sockets on each side, but fails to meet in middle.

Profrons: frontal line raised into prominent shield forming strongly-marked triangular frontal lobes on each side; median portion of whole frontal area distinctly bulbous.

Vertex: deep cleft extending from behind eyes on each side and under frontal shield seems to be peculiar to this species and without morphological significance.

Text-figure 16.



Scleropactes sp. viewed (A) from the side, (B) from the front.

Marginal line: forms posterior margin of head, becomes indistinct under eyes and lost before it reaches frontal line; reappears laterally low down.

Gena: smooth; deeply excavated under marginal line so that eyes are mounted on prominent shelf; genal fossa well marked.

Remarks: a head entirely different from the other conglobating forms. It is compressed antero-posteriorly, but not very strongly; the usual frontal crest is present, but the supra-antennary line is low on the face in its usual position and the antennary tubercle is in the position characteristic of the *Philoscia*-type. This specimen was described from Budde-Lund's material (British Museum), and is there labelled "*S. cavifrons* B.-L.," but no description of it seems to have been published.

18. SPHÆRONISCUS sp.

Very similar to *Scleropactes*. Also possesses a vestigial supra-antennary line which overhangs the antennal sockets. Side view very similar, but the head is more compressed antero-posteriorly and the upper surface is somewhat rectangular. The frontal line is very distinct, but the frontal shield is pressed back on the head and fused with it, so there is no crest or lateral lobes. This specimen was described from Budde-Lund's material (British Museum), and is there labelled "*S. intrusus* B.-L.," but no description of it seems to have been published.

19. PERISCYPHIS RUFOCAUDA B.-L. (Text-fig. 17.)

Clypeus: set off from face and strongly rolled; not distinctly separable from face; lateral processes large, projecting, and on inner side of antennal sockets.

Frontal lamina: middle part entirely obliterated; antennal sockets well defined and protuberant.

Antennary tubercle: not defined, but obviously combined with lateral lobes of frontal line under eyes.

Postfrons: confluent with profrons, as supra-antennal line is absent.

Profrons: frontal line defined at each side under eyes by sharp lateral crest, which passes on top of head and verges into another ridge behind and between the eyes. From its relation with the origin of the adductor mandibularis this is obviously the *interocular line* of lower forms. Median part of line obsolete.

Vertex: postorbital pits present behind interocular line.

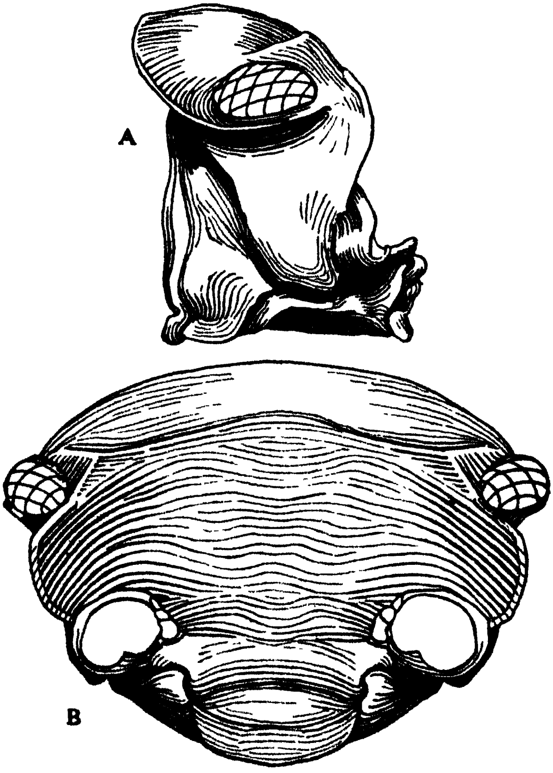
Marginal line: forms hind margin of head; strongly marked laterally and ends on ridge representing antennary tubercle and frontal lobe.

Gena: deeply recessed by first body-somite; genal groove and fossa present; lateral rib of maxillipedal somite narrow.

Remarks: a conglobating head related to *Cubaris*; the presence of the interocular line is a remarkable feature. The specimen described is labelled *P. rufocauda* B.-L., but does not conform with Omer-Cooper's description (1926) in respect of the frontal line, which is there described as "attenuated in the middle, but continuous across the head." It can scarcely be described as continuous in this specimen, which may therefore be the very nearly related *P. trivialis*.

Note on other species of Periscyphis.—There is great variation in the form of the ridge passing between the eyes (called by Omer-Cooper in his valuable revision (1926) the "marginal" line) in this genus and a statement of its homologies in each species seems to be desirable. A comparison with *Cubaris* makes it evident that the side lobes of the head are equivalent to the corners of the frontal shield of that genus (which correspond to both antennary tubercle and lateral lobes of such a genus as *Armadillidium*). The anterior pharyngeal processes are attached immediately in line with a prolongation of the internal edges of these side lobes, and, in many species, *well in front* of the line between the eyes. When this line (which is always broken in the middle) is present, its relations with the adductor mandibularis and anterior pharyngeal processes show it to be the

Text-figure 17.



Periscyphis rufocauda viewed (A) from the side, (B) from the front.

homologue of the interocular line of *Ligia*, an unexpected feature in a higher terrestrial Isopod. Species which have a true frontal line and a "frontal line" which is really the interocular line must therefore be carefully discriminated between. In any case, Omer-Cooper's term "marginal line," which has been employed by other authors for the line at the side and back of the head, cannot be used for this line without causing confusion. The condition found in all species described by Omer-Cooper is given below:—

P. trivialis: frontal line slightly developed at each side under eyes; absent in mid-line; fused at side with antennary tubercle; laterally marginal line nearly reaches antennary tubercle and lateral lobe. On each side of vertex, behind and between eyes, a short interocular line.

P. vittatus: antennary tubercle and lateral lobe feebly developed; no interocular line.

P. civilis: similar to above.

P. cavernicola: similar to *P. trivialis*, but interocular line is obsolete.

P. undulata: antennary tubercle and small portion of frontal line returning inwards, absent in mid-line; interocular line visible as short ridges on inner side of eyes.

P. albescens: similar to *P. trivialis*.

P. nigricans: similar to *P. trivialis*.

P. limbata: antennary tubercle strong and lateral portions of frontal line well developed; interocular line present.

P. pulcher: interocular line very well developed; frontal line ?

P. convexus: antennary tubercle and lateral lobe well developed; frontal line nearly meeting in middle; no interocular line; frontal shield bulging, but without defined median carina.

P. subtransversus: antennary tubercle little developed, but frontal line is well raised under eyes and runs into interocular line between eyes; in mid-line both are absent, but the anterior pharyngeal processes are attached in front of the prolongation of the interocular line.

P. latissimus: frontal line developed as in *Cubaris*; antennary tubercle and lateral lobes well developed; no interocular line.

20. SAIDJAHUS CREPER B.-L.

This head might belong to *Periscyphis limbata* Omer-Cooper. Antennary tubercle and lateral portion of frontal line are well developed; interocular line present at each side inside eyes; both obsolete in middle.

21. SUAREZIA HETERODOXA (Dollf.).

Of the *Periscyphis*-type, but lateral lobes and frontal line are ill-developed laterally, and the interocular line is far forward so as almost to join the frontal line in front of the eyes. The frontal line is entirely obsolete medianly, but the upper margin of the profrons is shown by the change in character in the granulations of the surface and the point of attachment of the anterior pharyngeal processes.

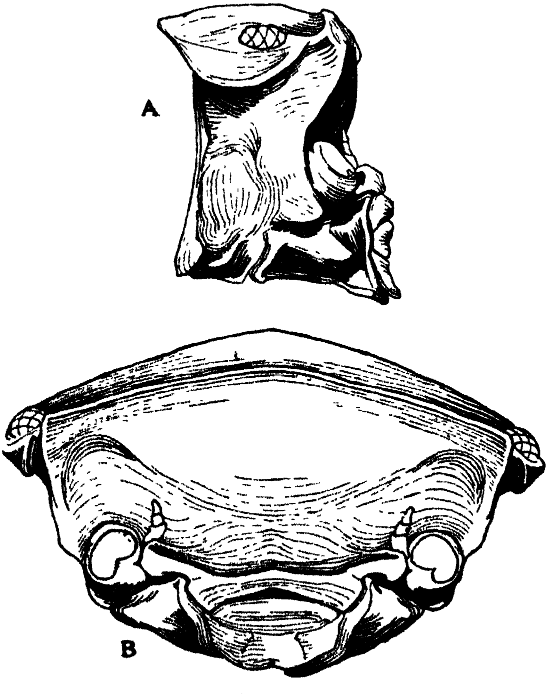
22. Microcercus anomalus Gerst.

A head intermediate between *Periscyphis* and *Cubaris*, with complete frontal shield of *Cubaris*; the clypeus small, rolled, and with moderate lateral processes, and the very narrow maxillipedal somite as in *Periscyphis*. No interorbital line; gena little grooved, very much shortened antero-posteriorly.

23. Cubaris officinalis (Desm.). (Text-fig. 18.)

Clypeus: set off from face and pronouncedly rolled; lateral processes greatly expanded, grooved off from body of clypeus and

Text-figure 18.



Cubaris officinalis viewed (A) from the side, (B) from the front.

lying to inner side of antennal socket; both deeply excavated dorsally; line of division from face marked by faint groove.

Frontal lamina: middle portion marked off from face by faint groove, but almost obsolete; antennal sockets set far on edge of head, wide apart and protuberant.

Antennary tubercle: lower edge marked by excavation on lateral corners of frontal shield, upper edge only faintly separated from shield. (Reference to this structure in *Armadillidium* makes *Cubaris* more intelligible.)

Postfrons: confluent with profrons, as supra-antennal line is absent.

Profrons: frontal line mounted on high crest, which forms triangular lobes at each corner; whole frontal area flat and expanded.

Vertex: very broad and narrow, anterior and posterior edges parallel.

Marginal line: forms hind border of head, passes under eyes, and is lost on lateral corner of frontal shield; not visible laterally.

Gena: high and narrow; deeply recessed under lateral line for first free thoracic somite; deep genal fossa.

Remarks: the most modified conglobating head; very flat from back to front and almost disc-shaped: supra-antennal line lost and frontal area lifted high up. The head of *Eubelum* is so close to the above as to require no separate description.

Anchicubaris Collinge, has the *Cubaris* type of head; antennulæ are present in the type-specimens, and not absent, as stated in Collinge's diagnosis.

24. CALMANESIA METHUENI Cllge.

Of *Cubaris*-type, although with individual modifications. The frontal shield is interrupted in the mid-line; it is more pronounced and is leant forwards; the lateral processes of the clypeus are massive and produced upwards into substantial knob-like projections which are not excavated above.

25. ARMADILLIDIUM VULGARE (Lat.). (Text-fig. 19.)

Clypeus: set off from face and somewhat rolled; no distinct separation from face in mid-line; lateral processes large, but not greatly expanded as in *Cubaris*; slightly excavate above and interrupted in mid-line.

Frontal lamina: middle portion obsolete, but faintly distinguishable as semicircular area; median groove above this area; antennal sockets widely separated and well defined, but not protuberant.

Antennary tubercle: forms high well-defined ridge over antennal socket, and supra-antennal line overshadows, at each side, antennal sockets.

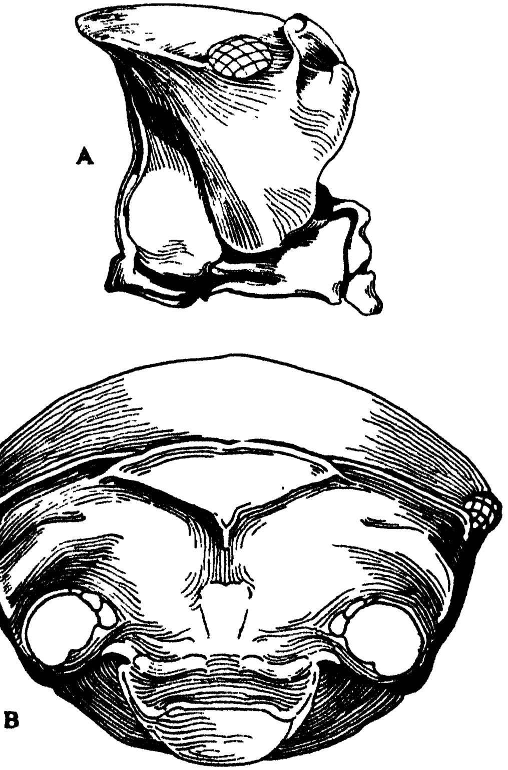
Postfrons: not distinctly demarcated from profrons, although supra-antennal line is distinct laterally and over antennary tubercle.

Profrons: provided with median triangular shield, which surpasses in mid-line the frontal line; this line is otherwise distinct, and raised on a crest with lateral lobes as in *Cubaris*.

Marginal line: forms hind border of head; well marked laterally behind eyes, but becomes lost anteriorly.

Gena: deeply recessed in position of genal groove for first free thoracic somite; genal fossa well marked.

Text-figure 19.



Armadillidium vulgare viewed (A) from the side, (B) from the front.

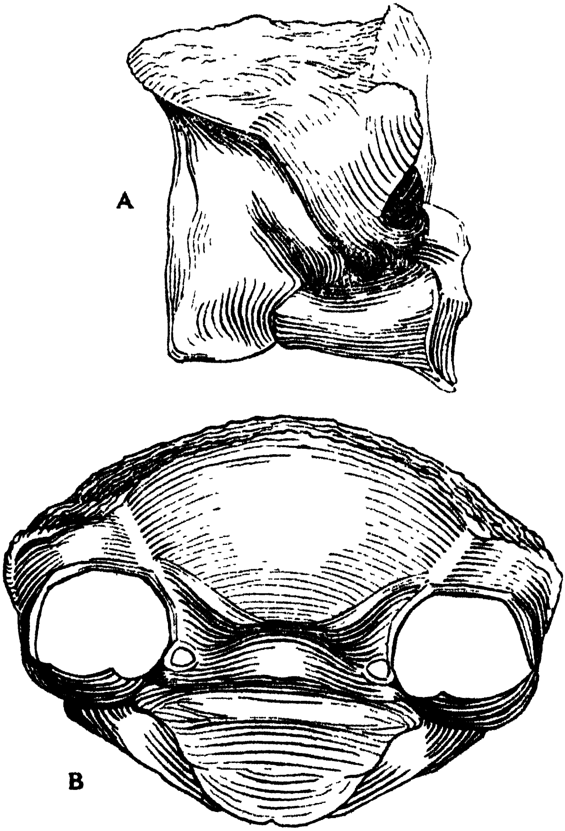
Remarks: a highly-modified conglobating type of head. The face could be interpreted differently from the above, if it be supposed that the postfrons has been lifted high up on the face so that the supra-antennal line runs over the border of the median triangular shield. A line is found in that position continued on each side by a faint groove on to the antennary tubercle. Such an interpretation, although possible, seems less probable than that given above.

Eluma cœlatum (Miers) is also a typical *Armadillidium*.

26. Platyarthrus hoffmanseggi Brandt. (Text-fig. 20.)

Clypeus: fused above with frontal lamina, rather bulbous; lateral processes small and weak.

Text-figure 20.



Platyarthrus hoffmanseggi viewed (A) from the side, (B) from the front.

Frontal lamina: middle portion defined above by a moderately deep groove in mid-line and slight groove elsewhere; fused below with clypeus; antennal sockets flat on face, overhung above by supra-antennal line and frontal lobes.

Antennary tubercle: not patent.

Postfrons: separated from profrons by well-marked supra-antennal line which curves down in mid-line.

Profrons: area limited above by indistinct frontal line marked by line of tubercles; frontal lobes encroach on face and are bulbous below so that they are in contact with supra-antennal line over antennal sockets.

Marginal line: forms hind border of head; distinct laterally, and continued downwards as in *Porcellio*.

Gena: slightly concave; genal fossa well marked.

Remarks: a head on the *Porcellio* line, but showing more primitive characteristics and special modifications.

Leptotrichus panzerii (Aud.) is nearly related to the above. The clypeus, however, is not bulbous, the supra-antennary line is scarcely distinguishable, and the marginal line is carried further forward laterally before dipping down.

5. *References.*

JACKSON, H. G. 1926. The Morphology of the Isopod Head. Part I. The Head of *Ligia oceanica*. Proc. Zool. Soc. Lond. pt. III. pp. 885–911 pls. i.–iv.

OMER-COOPER, J. 1926 A Revision of the Genus *Periscyphis* Gerst. Proc. Zool. Soc. Lond. pt. II. pp. 349–400, text-figs.

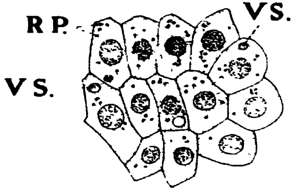


Fig.1.

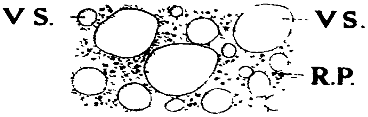


Fig.2.

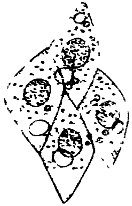


Fig.3.

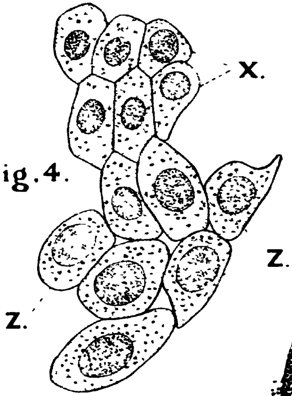


Fig.4.

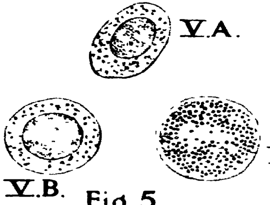


Fig.5.

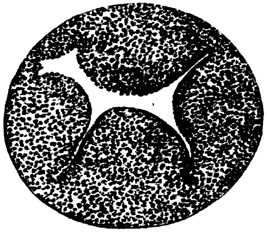


Fig.6.

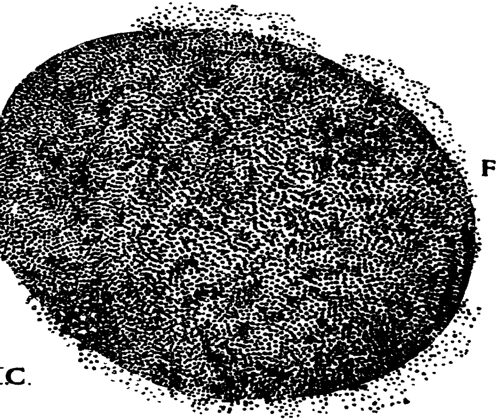


Fig.7.

Dinocampus (*Perilitus*) *rutilus*. Ness.

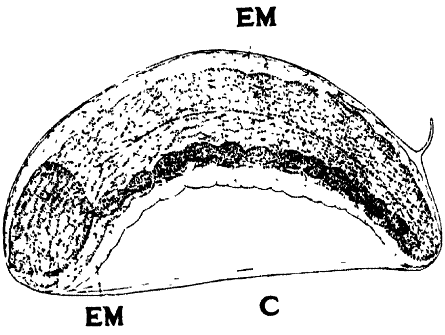


Fig 1

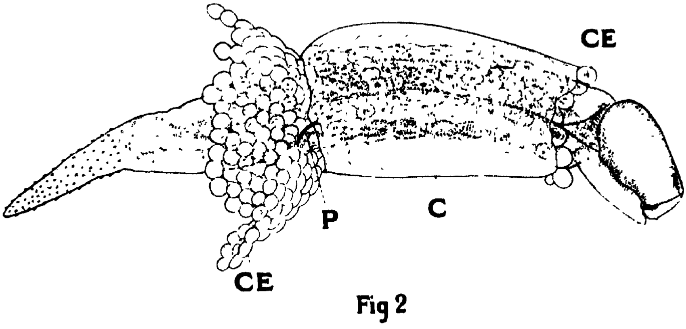


Fig 2

DINOCAMPUS (*PERILITUS*) *RUTILUS.* NESS.

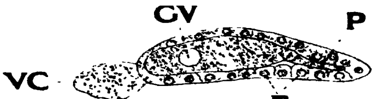


Fig 1

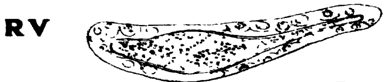


Fig 2

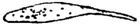


Fig 3

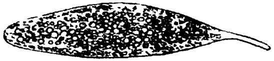


Fig 4

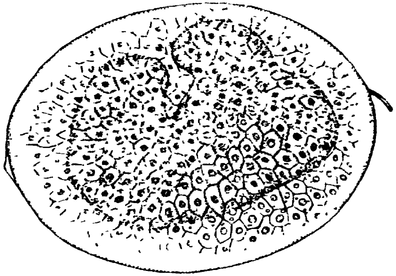


Fig 6

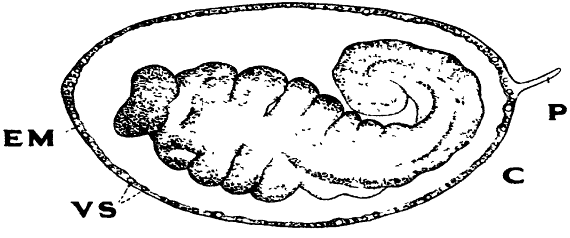


Fig 5

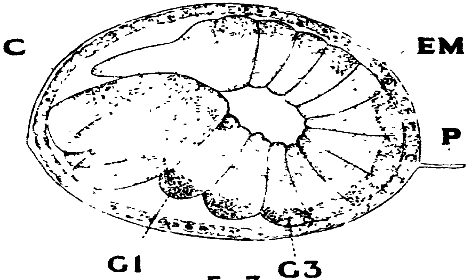
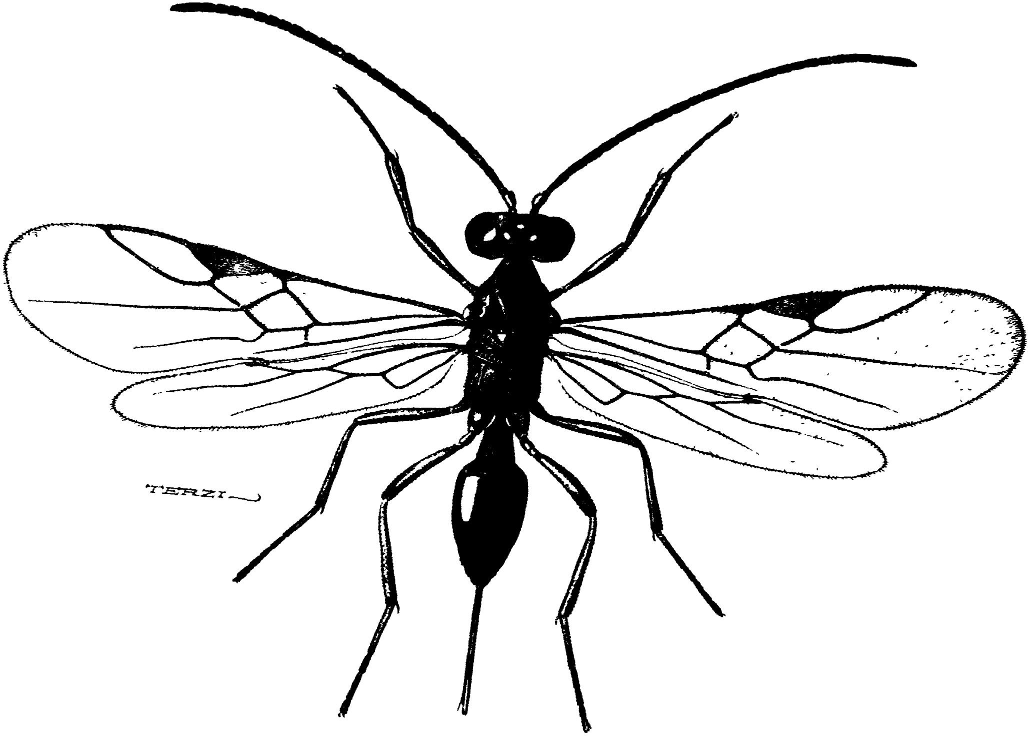


Fig 7

Dinocampus (Perilitus) rutilus. Ness.



Dinocampus (Perilitus) rutilus. Ness.

22. The Biology of *Dinocampus* (*Perilitus*) *rutilus* Nees, a Braconid Parasite of *Sitona lineata* L.—Part I. By DOROTHY J. JACKSON *.

[Received January 18, 1928: Read March 20, 1928.]

(Plates I–IV.†)

CONTENTS.

	Page
Introduction	597
Systematic Position of the Genus *Dinocampus*	598
Notes on Literature regarding Parasitism in the Genera *Dinocampus* and *Perilitus*	598
Notes on Literature regarding Parasitism of other Euphorids.	603

Dinocampus (*Perilitus*) *rutilus* Nees :—

Outline of Life-history	603
Methods of Rearing	604
Distribution	605
Observations on Imago	606
Habits of Imagines	608
The Egg	613
The Embryonic Membrane	617
Summary	626
Bibliography	627
Explanation of the Plates	629

INTRODUCTION.

Dinocampus (*Perilitus*) *rutilus* Nees is parasitic in the larval stage upon the adult weevils of *Sitona lineata* L., and has also been bred from *Sitona hispidula* F. Its parasitism was first discovered by the writer in 1919 whilst a study was being made of the bionomics of those species of *Sitona* which are injurious to leguminous crops. This work necessitated the dissection of large numbers of weevils in order to examine their reproductive organs, and it was then noticed that several of the beetles collected in the field contained within their abdomen a single parasitic larva. A little later full-grown Hymenopterous larvæ were found wriggling about in the boxes in which the adult *Sitona* were confined. Several of the larvæ died, but others succeeded in forming compact cocoons of white silk, from which the imagines were duly reared. They were submitted to Mr. G. T. Lyle, and identified by him as *Perilitus rutilus*. No observations had hitherto been recorded upon the parasitism of this insect, and it was thought that an investigation of its life-history would be of interest from the viewpoints of both pure and applied entomology. The series of observations on which this paper is founded was commenced in 1919, and has been continued for several years in order to obtain sufficient material for the study of the different instars. This work has been undertaken with the object of presenting a full account of the post-embryonic development of this species. Since the larva undergoes marked changes in structure during its life, special attention has been paid to its external anatomy. From the economic aspect alone it is of importance to be able to identify the insect in its different stages, and for this reason it has been found necessary to supplement the descriptions with numerous figures. The internal anatomy of the insect in its various instars has not been dealt with, excepting when some understanding of its structure is necessary in explaining the habits of the larva. Since the results of an investigation carried out on the lines indicated cannot be recorded except at some length, it has been found advisable to divide the paper into two parts. The first part is devoted mainly to the adult insect, the egg, and the curious development of the cells of the embryonic membrane. In the second part the larval and pupal stages are described; an account is also given of the seasonal history and the effects of parasitism on the host.

---

* Communicated by Prof. F. BALFOUR-BROWNE, F.Z.S.

† For explanation of the Plates, see p. 629.

I am indebted to Prof. F. Balfour-Browne for his criticism and advice in regard to the preparation of this paper, and my thanks are due to Dr. A. D. Imms for many helpful suggestions during the course of this research. At the Imperial Bureau of Entomology I have attained access to numerous papers on Hymenopterous parasites, and I wish to acknowledge my appreciation of the valuable assistance that has thus been rendered to me.

Systematic Position of the Genus Dinocampus.

The genus *Dinocampus* belongs to the Euphorinæ, a subfamily of the Braconidæ. It was erected by Förster in 1862 to receive those species of *Perilitus* in which the first cubital areolet of the fore wing is separated from the first discoidal. Marshall (1887), however, does not treat *Dinocampus* as a separate genus from *Perilitus*, and I have previously (1920–24) referred to this Braconid as *Perilitus rutilus*. Mr. Lyle has since informed me that the species ought rightly to be called *Dinocampus* (*Perilitus*) *rutilus*.

Notes on Literature regarding Parasitism in the Genera Dinocampus *and* Perilitus.

The two genera are widely distributed and the parasitism of a number of species has been recorded. As a rule these Braconids are parasites of the adult beetles, but in a few cases they have been recorded as attacking the larvæ also. The published data on the parasitism of the different species of both genera are here briefly summarized. It will be seen that the bionomics of the species differ in many important points, and that Coleoptera of widely-separated families serve as hosts.

Dinocampus (*Perilitus*) *falciger* Ruthe.—Very little is known in regard to the life-history of this species. The few existing records show it to be a parasite of Chrysomelid beetles of the genus *Timarcha*. Marshall (1887, pt. ii. p. 76) notes the presence of a specimen of this Braconid in the British Museum, ticketed "the larva from a living *Timarcha coriaria* F." Bignell (1891) records the rearing of this species from an imago of *Timarcha tenebricosa* collected in Devon, and he observed that 41 larvæ emerged from the beetle. A still older observation relating to the breeding of twenty small unnamed Braconids from *Timarcha tenebricosa* is reported by Sichel (1854) from France, and is probably referable to the present species.

Dinocampus coccinellæ Schrank.—The parasitism of this species was observed by Audouin in 1839 (see Westwood, 1840, p. 142), and its habits have attracted the attention of many entomologists since. It is referred to by these writers under a variety of names such as *Centistes americana*, *Dinocampus americana*, *D. terminatus*, *Perilitus americana*, and *Euphorus sculptis*. Its synonymy is discussed by Cushman (1922), who states that the insect was first described by Schrank in 1802 as *Ichneumon coccinellæ*. Observations have been made on the life-history of this species by Ratzeburg (1852) in Germany, and by Glover (1877), Riley (1888), Weed and Hart (1889), Hopkins (1890), Cushman (1913), and Timberlake (1916) in America, and a very interesting paper has been published recently by Balduf (1926). This writer mentions that this insect has been recorded also from New Zealand. Its occurrence in the Hawaiian Islands is mentioned by Timberlake (1917), and Tullgren (1916) gives some observations regarding its life-history in Sweden. Oglobin (1913) deals at some length with the bionomics of this insect in Russia. *Dinocampus coccinellæ* is a parasite of ladybirds (Coccinellidæ), and has been recorded from a number of species. It is always a parasite of the perfect insect, but Cushman observed the female attempting oviposition in larvæ as well as in adults of *Megilla maculata*. Only one larva is recorded as developing to maturity in each host. Oviposition is effected principally in the apex of the abdomen of the beetle. Three larval instars were distinguished by Balduf. The larva when full-grown emerges from the dorsal surface of the abdomen from the suture between the 5th and 6th segment. It then spins its cocoon beneath the body of its host on the surface on which the beetle is resting. The latter appears to remain in a quiescent condition astride the cocoon. According to Balduf, the ladybird usually dies about a week after the emergence of the larva. Timberlake (1916) gives a very interesting account of the recovery of the host in certain cases after the parasite had emerged, and shows that the beetle may even commence oviposition after an interval of 22 days. The same writer, moreover, succeeded in rearing two generations of *D. americanus* (*coccinellæ*) from the same individual host.

Dinocampus sp. is recorded by Moore (1913–14) from ladybirds in South Africa.

Dinocampus sp.—Shtcherbakov (1916) notes that an unnamed species of *Dinocampus* is an internal parasite of *Apion* in Russia.

Perilitus æthiops Nees.—I have already recorded the rearing of this species from an adult *Sitona hispidula* F. (1922, p. 105). Only one specimen was obtained. The host was collected at Invershin, Sutherland, on 21st September, 1921. The cocoon of the parasite was observed about a week later, and the imago emerged from it on 16th October. The cocoon is of white silk faintly tinged with pink, and was formed amongst the sterilized moss which had been placed in the receptacle in which the beetles were kept. Speyer (1925) records this species as obtained by Kaufmann from *Phyllotreta vittula.*

Perilitus bicolor Wesm.—This species was reared by Kaufmann (1923) in Germany, but its identity was not established till after the publication of his paper. It was then recorded by Speyer (1925) as an imaginal parasite of *Phyllotreta atra, P. undulata,* and *P. vittula.*

Perilitus brevicollis Haliday.—This species is of economic importance in that it attacks the larvæ and adults of *Haltica ampelophaga* Guér., the well-known pest of vines. Its parasitism was first described in 1891 by Kunckel d'Herculais and Langlois from Algeria. These authors consider that there are two generations of the parasite in one year, one occurring during June and July in the larva of the host, and giving rise to parthenogenetic females; the other autumnal in the body of the adult beetles, hibernating in them, and producing both sexes in the spring of the following year. One larva only develops in each host larva, emerging when full grown from the anal extremity, rarely from other regions of the body. The oviposition of this species in larva and adult is briefly described; when attacking the beetle the ovipositor is inserted between the segments of the abdomen. The perfect insect is described at some length, but very little information is given in regard to the structure of the last instar larva, and the earlier instars are not mentioned. The proportion of parasitism amongst the host larvæ varied from 50 to 80 per cent. In later years no further papers appear to have been published on the life-history of this species. Very brief reference is made to it by Picard (1913) in Algeria and Feytaud (1917) in France. Picard considers *P. brevicollis* to be one of the most useful parasites of *Haltica.*

Perilitus cerealium Hal.—The breeding of this species from an adult of *Sitona sulcifrons* was recorded by the writer in 1922. This Braconid has since been reared from *S. flavescens* and *S. hispidula,* and the specimens have been identified by Mr. G. T. Lyle. Some data have been obtained regarding the life-history of this insect. The winter is passed in the body of the host, probably as a first instar larva. When full grown the parasite larva emerges from the beetle by rupturing the membrane around the anal aperture, and it sometimes spins its cocoon near the dead body of the host. The cocoons are slightly different in appearance from those of *Dinocampus rutilus*, being more oval in shape and less parallel-sided. Their surface is less smooth than that of *D. rutilus*, owing to the presence of many loosely-woven strands of silk. The colour also serves to differentiate the cocoon of this species, since, instead of being pure white as in *D. rutilus*, it is yellowish-white or pale straw-colour. The larvæ of the hibernating generation leave the host in April or May, and the imagines emerge in May or the beginning of June. A specimen of a summer generation was reared in the end of August. The imago emerges from the cocoon by an irregular opening at one end. In all, seven specimens were reared, all females. Two were placed with adult *Sitona lineata*, and these Braconids were observed to attempt oviposition in these weevils in exactly the same way as *D. rutilus*, but no evidence of successful parasitism was obtained from these experiments.

Perilitus eleodis Vier.—The records at present available show this species to a parasite of Tenebrionid beetles of the genera *Eleodes* and *Embaphion* in America (U.S.A.). It was described by Viereck in 1913 from *Eleodes suturalis*, and since then it has been bred by McColloch (1918–19) from *Eleodes tricostata* and *E. opaca*, and by Wade and Boving (1921) from *Embaphion muricatum*. Swenk (1923) also records it from *Eleodes opaca* in Nebraska, apparently from both larvæ and imagines. In every other case it is described as a parasite of the adult beetle. McColloch (1918) gives some particulars in regard to its parasitism of *Eleodes tricostata*. He states that as many as 124 larvæ have been obtained from one beetle, but that the average number infesting each host is 50. The larvæ emerged from the anal slit of the beetle, and the latter died 12 to 48 hours afterwards. In one case a female beetle was observed to lay three eggs on the day that she yielded 124 *Perilitus* larvæ. The cocoons were formed amongst the soil, which is webbed together. Actual oviposition was not observed, but McColloch considers that it is effected in the abdominal sutures and at the junction of the legs with the body. The female Braconids were observed clinging to the legs of the beetles and trying to gain hold of the ventral side of the abdomen. The efficiency of the parasite in the field was not definitely established, but from the available data McColloch estimates the average parasitism as 5 or 7 per cent.

Perilitus epitricis Viereck.—Little information is available in regard to the life-history of this species, and the few existing records show it to be a parasite of adult flea-beetles in the United States. Cameron (1915) has reared it from the Potato Flea-beetle, *Epitrix cucumeris*. He states that oviposition is effected the intersegmental parts of the abdomen. The parasites merged from a hole usually found in the anal regions of the host beetle. The control effected by this Braconid was considered negligible. Chittenden and Marsh (1920) record the rearing of this species from *Phyllotreta pusilla* and *P. vittata*, and the highest percentage of parasitism observed in the former host was 16 per cent.

Perilitus gastrophysæ Ashmead.—Ashmead described this species in 1888 from two specimens labelled as reared from *Gastrophysa cyanea* from Washington, D.C.

Perilitus leptopsi Viereck.—This species is recorded by Farrel (1919) as a parasite of the Apple-Root Borer Beetle, *Leptops hopei* (Curculionid), in Australia, but no further particulars are given.

Perilitus melanopus Ruthe.—In 1921 Speyer directed attention to the occurrence of a Hymenopterous larva in a weevil of *Ceuthorrhynchus quadridens* Panz. in Germany. This species was identified later as *Perilitus melanopus*, and in 1925 Speyer published further observations upon it. Oviposition is effected in the apex of the abdomen of the host. The parasitized beetles in most cases continue to lay eggs, and only in advanced stages of parasitism does partial or complete castration occur. The larva emerges from the anus of the host and spins a white silken cocoon. This Braconid was observed to oviposit in other species of *Ceuthorrhynchus*, eggs or larvæ of the parasite being obtained from these beetles. Speyer does not consider that *P. melanopus* effects a substantial reduction in the number of *C. quadridens*. He gives a list in this paper of the Braconids which have been recorded as imaginal parasites of beetles. He includes in this list *Perilitus obfuscatus* as a parasite of *Orchesia micans*, but according to Elliot and Morley (1908, pp. 38 and 71) this record refers to *Meteorus obfuscatus* Nees.

Perilitus omophli Lesne.—This species was described by Lesne in 1892. He bred it from adult *Omophlus cæruleus*. The beetles were placed in a box, and small white cocoons were found later in a corner of the box. The larvæ remained near together to spin up, and the cocoons were arranged irregularly side by side. Both sexes of *P. omophli* were reared from these cocoons. The last instar larva is figured and described by Lesne.

Perilitus sp.—Speyer (1925) lists an unnamed *Perilitus* bred by Kaufmann from *Psylliodes chrysocephala*. The parasitism of this beetle, presumably by *Perilitus* sp., is discussed by Kaufmann. He states that the larvæ leave the beetles in April and May and spin their cocoons. The host dies after the emergence of the parasite. The reproductive organs of the female beetle gradually degenerate during parasitism, but those of the male host still harbour ripe spermatozoa towards the end of parasitism.

Perilitus sp.—A species of *Perilitus* was bred by the writer from *Sitona crinita* from Sudbury, Suffolk (1922, p. 113), and submitted to Mr. Lyle for identification. He informed me that it belonged to the genus *Perilitus*, but was probably an undescribed species.

Notes on Literature regarding Parasitism of other Euphorids.

Some records exist of the parasitism of species belonging to other Euphorid genera, and it is interesting to find that certain species are also parasites of adult beetles. Thus various species of the genus *Cosmophorus* have been reared from Scolytid beetles [Seitner & Nötzl (1925), Ruschka (1925)], and Marshall mentions (A, 1887) that *Euphorus pallidipes* has been bred from *Orchesia minor*. That the parasitism of the Euphoridæ is not, however, confined to Coleoptera is shown by Menzel (1926) and Lean (1926), who have reared species of *Euphorus* from the Capsid *Helopeltis*.

DINOCAMPUS (PERILITUS) RUTILUS Nees.

Outline of Life-history.

Since only a portion of the life-history is dealt with in the present section of this paper, it will be advisable to give here a brief account of the bionomics of this insect. Both sexes of the Braconid are equally common. The female effects oviposition in the apical region of the abdomen of the beetle. The egg increases greatly in size after oviposition. The larva, on emerging from the egg, occurs free in the body-cavity of the beetle. Only one larva attains maturity in each host. A sure indication of parasitism is afforded by the large numbers of opaque white globules which are always present in the body-cavity of a beetle containing a parasitic larva. These globules have frequently been mistaken for disorganised fat-body of the host. They are, in reality, the dissociated cells of the embryonic membrane of the egg of the parasite. They become of large size, absorbing fatty matter from the body-fluid of the host, and they constitute the principal food of the larva in its later stages. Five larval instars have been observed. When full grown the larva emerges from the host by rupturing the membrane around the anal aperture. It then forms a compact white silken cocoon, which it covers over with particles of soil. Before moulting into the pupal state, the larva expels the waste food-matter accumulated during its parasitic life. This excrement is enclosed in a long membranous sac which previously lined the mid-intestine, forming a sort of peritrophic membrane. The weevil dies soon after the emergence of the larva. The reproductive organs of the female beetle are rendered functionless by parasitism, but the testes of the male may contain living spermatazoa after the parasite has emerged. There are from two to three generations of the Braconid in the year. During the summer the development from egg to fully-grown larva occupies a month, in the autumn and winter it may take as long as eight months. The time spent in the cocoon varies from three weeks to over a month.

Methods of Rearing.

The cocoons of the parasites were obtained from adult *Sitona lineata* which were collected from the field throughout the year and kept in captivity until the parasite larvæ emerged from them. As the percentage of weevils parasitized was rarely high, large numbers of beetles had to be collected, and various methods of housing them were tried. The most satisfactory results were obtained by using flower-pots about eight inches in diameter. Each pot was lined with dark cloth, the edges of which were securely fastened round the rim of the pot with string. Bottles of water containing clover or bean-shoots for feeding the weevils were suspended into the pot in wire holders, the latter being supported by string round the rim of the pot. A muslin sleeve, high enough to cover the leaves, was then affixed to the pot and tied together at its free end with string. A very secure and convenient receptacle was thus obtained for housing the weevils. The food remained fresh for many days, and when it required renewing, the bottles could be lifted out of the wire-holders and replenished. The white cocoons of the Braconid were spun upon the dark cloth, and therefore easy to see. They were usually formed low down in the cloth bag, and the wire supports prevented the bottles from crushing them. The cocoons were removed directly they were found by cutting out the cloth on which they were formed, thus avoiding injury. The holes thus made were patched, and the same receptacle was available for continued use. The pots were kept in an outside insectary, and in winter it was found advisable to add dried moss (previously sterilized) to the pot to give the weevils more shelter. It was also necessary to wrap felt round the bottles to protect them from the frost.

Each cocoon was placed in a separate receptacle, so that the resultant imagines could be used for bisexual or parthenogenetic reproduction as desired. The cocoons were kept in small glass tubes open at both ends, the open ends being covered with muslin held in place by elastic bands. These tubes were inserted in holes in a wooden framework, the lower ends of the tubes resting on a sheet of perforated zinc attached to the woodwork. This framework was placed over a large tin containing damp moss, and the cocoons were thus kept in a slightly moist atmosphere without being in contact with the wet moss.

On emergence from the cocoons the female Braconids were placed with adult *Sitona lineata* in which to oviposit. The weevils used for this purpose had to be bred in captivity, as specimens collected in the field were liable to be already parasitized by this or by other species of Braconids. The larvæ of *Sitona lineata* feed on the root nodules of peas and beans, and the breeding of these weevils in sufficient numbers has constituted one of the principal difficulties of the research. There is only one generation of *Sitona lineata* in the year; therefore, if sufficient bred specimens were not obtained one season, all the work of rearing parasites and beetles had to be started afresh next year. Moreover, it sometimes happened that in rearing these beetles in captivity their development was delayed, and the parasites would emerge from their cocoons and die before the beetles were ready for them. The rearing of parasites and beetles was carried out in Ross-shire; but I frequently obtained supplies of parasitized beetles from England, and in this case especially the emergence of parasite and host often failed to coincide, as in the north of Scotland the weevils emerge about a month later than in England, and the Braconids reared from English weevils emerged, in consequence, about a month too soon

Fortunately it was possible, when sufficient bred weevils were not available, to use for rearing the parasite specimens of *S. lineata* which had been collected in the field six months previously, since after that lapse of time only the unparasitized individuals would be left alive; but the drawback to this method was that the weevils reared were already old, and often died before the parasite had completed its development.

Even when the female *Dinocampus* and the bred weevil were placed together, successful parasitism was not ensured, for the Braconid often failed to effect oviposition in the weevil, and one would keep and feed such a weevil for weeks or months, only to find on the day of dissection that it had never been parasitized. The bred weevils were placed with the Braconid for a day or longer, according to whether or not the female *Dinocampus* showed active tendency towards oviposition. As soon as one had reason to hope that an egg had been deposited safely, the weevil was removed and another victim was offered to the parasite. The beetles which had been with the Braconids at different times were kept separately, so that when they were dissected the exact age of the egg or larvæ could be ascertained. The beetles were dissected at various intervals after oviposition, and by this means all stages of the parasite were eventually obtained.

Distribution.

According to Marshall (B, 1891) this species occurs in Germany, Belgium, Holland, and England, and probably in all Europe. Szépligeti (1904) gives as its distribution "Europa fere tota." In his British Braconidæ, Marshall (1887) states that this species is rather common throughout the country. It is probably widely distributed in all parts of the British Isles. I have obtained it from the following localities:—Alness and Evanton, Ross-shire; Beauly, Inverness-shire; Hull; Cambridge (from Mr. J. Balfour-Browne); Sudbury, Suffolk (the weevils were sent me by Mr. B. S. Harwood); Haslemere, Surrey; Wye, Kent; Long Ashton, Bristol (weevils from Mr. Miles).

Observations on Imago.

A description of the male and female of this species is given by Marshall (1887, pt. ii. pp. 73–74).

Variation in Size and Coloration.

The difference in colour between the two sexes is strongly marked, the male being much darker than the female. Variation has been observed in the coloration of both sexes. Some males are darker than others, and a few females taken at Cambridge were unusually brightly coloured. Hase (1922) has observed great variation in the coloration of the imagines of *Habrobracon brevicornis*, and he has found that, by rearing this species in high temperatures, only lighter-coloured individuals were produced and the formation of black pigment appeared to be prevented. In *Dinocampus rutilus* the size is also very variable. Measurements have been made of 34 set specimens across the fore wings from the tip of one to the tip of the other. In the females, measurements thus obtained varied in different specimens from 3·93 to 6·64 mm., and in the males from 3·99 to 5·93 mm. Similar variation in size has been noted by Hase in *Habrobracon*, and he finds that the small forms are produced through lack of sufficient quantity of food. Thus, when many larvæ are present in one host, those emerging last do not get sufficient food, and give rise to dwarf imagines. In *Sitona*, where only one larva can attain maturity in each host, this form of starvation cannot operate, but it is possible that the size of the Braconid may be influenced by the size and age of the host.

Proportion of Sexes.

In rearing *Dinocampus rutilus* from beetles collected in the field, it has been found that both sexes are equally common. Records have been kept of the sex of nearly 200 imagines reared; 97 were males and 94 females.

Parthenogenesis.

Unmated females of this species exhibit just as much activity in regard to oviposition as do mated females. The eggs laid by unmated females are fertile, and numerous weevils have been dissected which contained eggs or larvæ of virgin females. Owing to scarcity of material, many parthenogenetic specimens have had to be sacrificed for study of larval stages, and only 19 have been reared to the pupal or imaginal condition. All these have been males. These results are in striking contrast with those of Oglobin (1913), who has found that in *Dinocampus terminatus* (*coccinellæ*) parthogenetic reproduction produces females, and in the course of two years' observations he has not met with any males, though he states that they are known to the systematist. His results are confirmed by Balduf (1926), who has obtained no fewer than

60 imagines of this species, all females, and has in four instances reared females from beetles in which unfertilized females had oviposited. Many species of Braconidæ are known to be capable of arrhenotoky, and records of thelyotoky are less common. In *Pygostolus falcatus* Nees, another parasite of *Sitona*, I have myself reared three generations thelyotokously. I have never seen a male, though these are known to occur. In *Lysiphlebous tritici*, Hunter states that both males and females have been obtained by parthenogenetic reproduction, but that the male offspring predominate. Under natural conditions Hunter states that the females of this species are very much more abundant than the males, the ratio of males to females being 34 to 65. Webster's (1909) remarks on the parthogenesis of this species are very interesting. He states that experimental breeding has shown that a limited number of females could be bred parthenogenetically for three generations, but beyond that all the offspring were males. In *Habrobracon brevicornis*, Genieys (1925) states that unfertilized females produce only males, but Hase (1922) in one instance reared male and female offspring from an unmated female. The fertilized females of this species produced both males and females, and they frequently laid also sterile eggs. Genieys finds that the sexuality of the laying changes as soon as a female is fertilized, and if the female is mated to a feeble or exhausted male both sexes are at first produced, but latterly only males.

With *Dinocampus rutilus* I have been unsuccessful in rearing to the adult stage the progeny of females whose mating I have witnessed. Since, however, both sexes are equally abundant under natural conditions, it is probable that mated females produce males as well as females. This is known to be the case with many Braconids capable of arrhenotokous reproduction, though in some species the fertilized females gave more female than male offspring (Williard, 1920; Pennington, 1916). Shevirev (1913, A) believes that the mated females of species of *Pimpla* are able to regulate the sex of their offspring, and that female eggs are principally deposited in large host pupæ and male eggs in small pupæ. He finds that when large pupæ are offered, males can be quite excluded from the descendents of a given female, and when only small pupæ were supplied the percentage of males reared was greater than that of the females. In another paper (1913, B), however, the same writer (his name is here spelt Chewyreuv) refers to instances in which the female *Pimpla* have not manifested this supposed faculty of regulating the sex of their offspring, but he considers such cases exceptional. It is usually believed that the mated females of Braconids lay fertilized and unfertilized eggs, the former (diploid ?) giving rise to females and the latter (haploid ?) developing into males. It has, however, been shown that in the genus *Dinocampus* parthenogenesis in one species produces females and in another species males, and until the cytology of these insects has been thoroughly investigated, no conclusions can be drawn in regard to the method by which the sex of these Braconids is determined[*].

Habits of Imagines.

Feeding.—The imagines have been observed to feed upon the sticky substance occurring on the nectar-secreting disk of flowers of umbelliferous plants such as *Ægopodium*. On reaching the flowers the imagines have been observed to draw their mouths backwards and forwards on the nectar-secreting disk, and to move their palpi vigorously. They also appear to drink water from moist surfaces.

Movements.—Both sexes are active in their movements, walking rapidly and flying readily. When walking the wings lie folded along the back, but the male raises the wings when sexually stimulated. Both sexes spend much time in cleaning themselves, drawing their hind legs down over their abdomen and along their wings, cleaning their antennæ with their front legs and rubbing one leg with the other.

Longevity.—Various methods have been tried of keeping the imagines alive, but they appear to be short-lived. They have been kept out of doors in glass tumblers covered with muslin, and have been supplied with nectar-secreting flowers and sometimes with honey diluted with water. Wet cotton-wool was placed in the foot of the tumbler to provide moisture, but as the insects were apt to drown themselves in this, wet sand was substituted. The female Braconids were also provided with weevils of *Sitona lineata* to oviposit in. Despite such treatment, the average length of life for both sexes was about a fortnight, but many died much earlier. A few specimens, however, survived for over three or four weeks, and one female which reached the age of 33 days was observed to pursue weevils with intent to oviposit up to the day of her death. These observations were made upon specimens which emerged in August. Specimens which emerged in October and were kept indoors to protect them from frost rarely lived over a fortnight. Some of the imagines reared were mated, but others were not. The records are not sufficiently numerous to show whether mating affects longevity, but it happened that the longest-lived males and females were unmated ones[†]. About 24 hours before the Braconids died their antennæ began to droop, and were trailed behind or beneath them when they walked. When this happened the females evinced no further interest in the weevils, and death invariably followed.

---

[*] Since writing the above, the interesting paper by Muesebeck and Dohanian on the parasites of *Apanteles melanoscellus* (U.S. Dept. Agric., Bull. no. 1487, pp. 1–35, Washington, 1927) has come to my notice. These writers have also observed that different species of a genus may differ with regard to the sex of the progeny resulting from parthenogenetic reproduction, and they record instances of one species producing males and another females in the genera *Hemiteles*, *Pleurotropis*, and *Anastatus*. They state that in the thelyotokous species, *Hemiteles tenellus*, several pure lines of females have been obtained through 12 generations; and Orlov (Défense des Plantes, i. nos. 3–5, pp. 116–124, 1024) has bred parthenogenetically 22 generations of *Hemiteles areator*, rearing thereby 1238 females but no males.

[†] Prof. F. Balfour Browne, in his paper "On the Life-history of *Melittobia acasta* Walker; a Chalcid parasite of Bees and Wasps," Parasitology, xiv. 1922, p. 363, shows that the length of life of the female is enormously increased if mating is prevented.

In view of the success obtained by other writers (Doton (1911), Hase (1922), Willard (1920), Balfour-Browne, F. (1922)) in keeping Hymenopterous parasites alive for several months, the results here recorded are disappointing, but it is interesting to find that Oglobin (1913), working at *Dinocampus terminatus* (*coccinellæ*), states that the adults lived about 20 days in captivity; so perhaps about three weeks is the normal life of the adult *Dinocampus*. Balduf (1926) found that the imagines of *D. coccinellæ* (*terminatus*) lived only 4 or 5 days under cage conditions, but one individual, kept largely in the dark, survived for 18 days.

Copulation.—Mating takes place readily in captivity. It is difficult to know how recognition by the male of the presence of the female is effected. In some cases, on introducing a male into a tumbler containing a female, he will at once show signs of sexual excitement, though he may be some distance from the female. At other times he may be only a quarter or half an inch away from her, and yet take no apparent notice of her. When aware of her presence, often as the result of an accidental encounter, the male usually pursues her excitedly, raising his wings and moving his antennæ up and down. In such cases copulation is usually effected speedily in the following manner:—The male brings the tip of his abdomen forwards beneath his thorax until it reaches the genital orifice of the female, situated at the base of the ovipositor. The claspers are firmly pressed into slight depressions in the female's abdomen at either side of the genital opening, and coition is accomplished. The male then lifts his first and second pair of legs from the surface on which he is standing, and, swinging backwards, turns his body completely round, so that his under surface is in line with the dorsal surface of the female. In this inverted position he remains attached to the female, his fore and middle pair of legs in the air, and his weight slightly upheld by his hind pair of legs, which retain their original hold. The male remains in this position even when copulation takes place on the under surface of a horizontal support. In this case the male hangs head downwards, his wings still raised and the hind pair of legs resting behind and above him on the surface on which the female is standing. Only once has a male been observed to hold the abdomen of the female between his fore legs before copulating. Both insects remain, as a rule, motionless during coition, and if the female moves away the male is dragged behind. Copulation lasts from 10 to 90 seconds, and the male then removes himself, regains his normal position, and walks away with wings still raised.

I have been unable to discover whether the females may be mated more than once. A newly-mated female is still attractive to males, which pursue her in the usual fashion. The mated female, however, has frequently been observed to turn round and face the male, and even to pursue him in exactly the same manner in which she follows a weevil with intention to oviposit. Thus, in one instance, a male was following a newly-mated female and touching her with his antennæ, which he moved up and down with jerky beats. The female immediately turned and faced him, retreating before him with antennæ outspread, exactly according to the method she adopts when avoiding the approach of a weevil. Thus, walking backward and keeping just out of reach, she finally got rid of her pursuer. Females which have been mated for some little time appear to be less attractive to males. Thus a female mated four days previously was placed with an unmated male which paid no attention to her, though he encountered her repeatedly. The next day two more males were introduced with the same result, and the female was observed to pursue one as though it were a weevil. An unmated female was then substituted, and the attitude of the male entirely changed. Whenever he met her he raised his wings and commenced pursuing her, his wings fluttering and his antennæ waving, and, within six minutes of her arrival, he effected copulation. Immediately after this she was pursued by other males, including one of the individuals which had evinced no interest in the previous female. She, however, adopted the defensive (?) tactics described above, and a second copulation was not effected. Occasionally it happens that a female mated some days previously will arouse interest in one male but be unattractive to others. Thus a newly-emerged male was seen to pursue a female mated a week before, but the same female was entirely ignored by two other males which had been following a freshly-mated female.

A male that has once mated may, within a few hours, exhibit renewed interest in the same or another female, and it is probable that the male of *Dinocampus rutilus* is capable of several copulations, though so far the same male has only been observed to copulate twice. Old males which have been kept apart from females exhibit sexual activity when placed with females, and, in one case, such a male, while pursuing a female, encountered another male and attempted to copulate with it.

The males exhibit sexual activity the day they emerge, and the female may be fertilized directly she leaves the cocoon. A male was not observed to take any interest in a cocoon which contained a female in the act of emerging, but directly she was out he commenced to pursue her, and effected copulation twelve minutes later, before the female had succeeded in freeing her wings from her abdomen.

The attitude assumed by the male of *Dinocampus rutilus* during copulation appears to be rather different from that described in other Braconids, in which the male mounts the female or rests his fore legs upon her. In *Cosmophorus henscheli*, however, the copulatory attitnde of the male would appear from

Seitner and Nötzl's account (1925) to be very similar to that of *Dinocampus rutilus*. Lichtenstein and Picard (1918) state that the females of *Sycosotor lavagnei* do not appear to attract males after the first copulation, and Genieys (1925) has observed that the female of *Habrobracon brevicornis*, when once fertilized, forcibly repels the advances of other males. Shevirev, (A, 1913) has found that the females of species of *Pimpla* are only once fecundated, and refuse afterwards to copulate with other males. He applies the term "uninuptæ" to such species and "multinuptæ" to those species, such as *Theronia*, in which the females are fecundated repeatedly by many males.

Oviposition.—The female Braconid is ready to commence oviposition the day she emerges from the cocoon. Her task is not an easy one, as the weevil is so well protected by its hard chitinous integument; but a vulnerable region occurs at the apex of the abdomen between the tergite and sternite of the last abdominal segment, and it is here that oviposition is effected. The Braconid only appears to be aware of the presence of a weevil when quite close to it. She then stations herself immediately behind it and commences to follow it assiduously, advancing as the weevil advances and remaining motionless when the weevil stops. In pursuing the weevil the Braconid frequently moves her antennæ up and down, but, when waiting behind it, her antennæ are extended motionless on each side of her head and directed slightly forward. If the weevil turns round and commences to walk in the opposite direction the Braconid is in danger of being trampled upon, but she quickly retreats backwards, facing the weevil, and then, stepping to the side, takes up her position once more behind her intended victim. The pursuit may continue in this fashion for some time without any attempt being made to oviposit, but sooner or later, usually while the weevil is moving, the Braconid may be seen to raise herself suddenly on her hind legs and to bend her abdomen beneath her so that the dark valves of the ovipositor project well in front of her head. The orange-coloured ovipositor is then protruded through the valves, and directed with lightning-like rapidity at the apex of the abdomen of the weevil. When the weevil is moving, the Braconid effects oviposition while pursuing it, darting forward at the moment she strikes. If the thrust is well aimed, the ovipositor is plunged into the body of the weevil, apparently through or at the side of the anal opening. It is held there for an instant and then quickly withdrawn. I have once seen the ovipositor directed towards the junction of the 6th and 7th sternite, but do not know if oviposition was then achieved. If the Braconid strikes successfully, the weevil may be seen to start and walk rapidly as though disturbed; but very often the attempt at oviposition fails, and the ovipositor, missing its mark, glances off the hard sclerites of the beetle. At other times the weevil may be walking so quickly that it keeps just out of reach of the ovipositor. In such cases the parasite usually continues her pursuit, and may keep her abdomen for a little time bent beneath her ready to strike. A most favourable opportunity for oviposition is afforded when the weevil voids excrement. Just before the excrement is ejected the weevil extends the tip of her abdomen beyond the elytra. The Braconid instantly gets into position to strike, and as the waste matter is extruded darts her ovipositor into the anus. Another occasion on which the weevil is liable to attack is when it is about to fly. The elytra may be raised slightly several times before flying, and the membranous tergites of the abdomen are thus momentarily exposed. The parasite, still stationed behind the weevil, strikes just as the elytra begin to be raised and before they are lifted in the air. The ovipositor is directed to the membranous abdominal tergite in front of the pygidium (the propygidium). The Braconid has to be exceedingly quick in her movements to keep out of the way of the wings of the beetle, which may be spread with great rapidity and, if lowered, project on each side of the parasite.

The Braconid attempts oviposition at all times of the day, and has even been seen waiting behind a weevil at dusk. The presence or absence of sunlight does not appear to affect her activities. She continues to follow weevils intermittently throughout her life, and two females, which lived respectively for 26 and 34 days, were seen pursuing the beetles a few hours before their death. The parasite may make repeated attempts to oviposit in the same weevil, and, in consequence, many eggs may be laid in the body of the victim, though, as will be shown later, only one is destined to survive. Superparasitism occurs frequently in captivity if too few weevils be placed with the parasites. Beetles collected in the field rarely contain more than one egg or larva, though four larvæ and one egg have been dissected from one such individual. My observations do not indicate that the Braconid is capable of discriminating between parasitized and unparasitized beetles, but rather that she is ready to oviposit in whatever individual of *Sitona lineata* she chances to encounter, and eggs may be laid in beetles which already contain a well-grown parasite larva.

The oviposition of other species of the genera *Dinocampus* and *Perilitus* has been described by various writers, and would appear to be similar to that of *D. rutilus*. The most favoured region for attack is the apex of the abdomen, though attempts may be made to oviposit in other parts. Balduf's (1926) account of the oviposition of *Dinocampus coccinellæ* is very interesting. The Braconid finds the conditions for oviposition most suitable when the ladybird is moving, as the beetle then carries the abdomen raised up in an attitude favourable to attack, and, if the parasite finds the intended victim motionless, it will strike it with its antennæ, head, or legs to rouse it into running.

In the allied genus *Euphorus*, Menzel (1926) finds that the female of *Euphorus helopeltidis*, a parasite of the Capsid, *Helopeltis antonii*, oviposits by springing upon its victim, bending the abdomen downwards and forwards, and plunging the ovipositor into the abdomen of the bug. This Braconid was observed to select the very youngest *Helopeltis* stages and to avoid the older ones and those that were already parasitized, but, as Menzel points out, this discrimination between parasitized and unparasitized specimens is more possible with the thin-skinned *Helopeltis* than with beetles.

In another Euphorid, *Cosmophorus henscheli*, a parasite of the beetle *Pityophthorus henscheli*, the oviposition as described by Seitner and Nötzl (1925) is entirely different from that of *Dinocampus rutilus*. The Braconid endeavours to seize the beetle with her mandibles and bring it into the right place. Finally, when she has brought the beetle face to face with her, she grasps it behind the thorax with her mandibles and presses it to the ground, thereby rendering it defenceless. The ovipositor is then unsheathed and driven under or at the side of the head of the beetle, probably into the mesothorax.

The Egg.

The Ovarian Egg.—The ovaries of several females of *Dinocampus rutilus* have been examined, and it has been found that the ovarioles vary in number and are seldom of the same number in each ovary. Specimens have been found in which the numbers of ovarioles were as follows:—7 and 8, 7 and 5, 7 and 6, and 6 and 6. The ovaries are well developed in the newly-emerged female. Fifty-four fully-developed ova and eighteen immature ova were found in the ovaries of a female which was dissected a few hours after emergence from the cocoon. In a six days' old female which had laid no eggs, 74 fully-developed ova were counted and immature ova were also present. The fully-developed ova are to be found in the lowest part of the tube. I was unable to detect a follicle sheath round those just ready to be laid, but the eggs situated a little higher up in the ovariole have a distinct follicle sheath (Pl. II. fig. 2). The germinal vesicle of such eggs is not visible in unsectioned specimens, but is very distinct in eggs of an earlier stage (Pl. II. fig. 1). The egg, when ready to be laid (Pl. II. fig. 3), measures from 0·2 mm. long by 0·036 mm. broad to 0·24 mm. by 0·044 mm. One end tapers to the long pedicel; the other end is bluntly rounded. Difficulty was found in distinguishing the micropyle, but it is perhaps represented by a minute mark, usually obliquely placed appearing like a break in the chorion and situated in the middle of the broad end of the egg. This mark was observed in many specimens. According to Tower (1915) the micropyle in the egg of *Apanteles militaris* Walsh is situated at this point. The chorion of the mature egg is very distinct and relatively thick. Strongly refringent particles of irregular shape may be distinguished amongst the faintly granular protoplasmic contents of the egg. The eggs are situated in the ovarioles, with their petiolate end towards the oviduct and their broad end nearest the head of the insect. Although after oviposition, the egg increases greatly in size and loses its characteristic shape, the two poles can still be distinguished, as the petiole persists. It was observed that the head of the embryo developed at the end furthest removed from the petiole, and this is in accordance with the law of orientation described by Hallez (1886). Grandori (1911) also states that the pedicellate pole of the egg of *Apanteles glomeratus* corresponds to the posterior extremity of the future embryo. It is therefore surprising to find that Balduf (1926) describes the petiolate end of the egg of *Dinocampus coccinellæ* as cephalic.

It is well known that in certain ectoparasitic Ichneumonidæ, e.g., *Paniscus*, the pedicel of the egg is threaded by the ovipositor through the skin of the host, and when the ovipositor is withdrawn the egg remains attached to the host by the pedicel. In such forms, however, the egg is not enclosed in the ovipositor during the act of oviposition, but is attached to it by the pedicel. Grandori has suggested that the pedicel of the egg of *Apanteles* serves to hook the egg to the viscera of the host, and so prevent it from being swept about and damaged by the circulating fluid of the host. In *Dinocampus rutilus* it is not easy to understand how the petiole could serve for the attachment of the egg, unless, during laying, the pointed end should happen to pierce the viscera of the host. Thus Speyer (1925) has found on two occasions that the egg of *Perilitus melanopus* was hanging on to the reproductive organs of the host. It is probable that the petiolate structure of the egg serves principally to facilitate oviposition, as the narrow pointed end of the egg will pass first down the ovipositor and through the integument of the beetle.

The small size of the egg must undoubtedly be of advantage when oviposition has to be effected in a quickly moving host, and, as Oglobin (1913) points out, the smallness of the eggs of such endoparasites is compensated for by their expansion after oviposition. In the ectoparasite *Habrobracon brevicornis*, Hase (1922) states that the egg is large, and that its size is in striking contrast with that of *Apanteles glomeratus*, which is laid within the body of the host.

The Egg after Oviposition.—No research has been carried out on the embryology of *Dinocampus rutilus*. Observations have been made on the general appearance of the egg from shortly after oviposition till the emergence of the larva. The eggs have been mounted fresh in normal salt solution, and the drawings have been made with the help of a camera lucida. The eggs studied have been produced by the autumn and not by the summer generation of the parasite. They have thus been laid at various dates in October, and their development has been much slower than is the case with eggs laid during the summer. The eggs occur in the abdominal cavity of the beetle and the newly-laid eggs are hard to find owing to their small size. The egg gradually undergoes a great increase in size, the chorion expanding and liquid substances being absorbed from the body-fluid of the host. At first the breadth of the egg increases more than its length. Thus an egg dissected from a beetle 43–49 hours after oviposition was of the same length as the mature ovarian egg but 20 μ broader, the greatest breadth occurring in the middle, and the egg thence tapering to the two extremities. Later the egg becomes larger and more evenly swollen throughout, with the exception of the pedicel, which remains always the same size. Balduf (1926) states that the pedicel of *Dinocampus coccinellæ* becomes gradually absorbed, and disappears when the egg has attained its full size. In *D. rutilus* I have, however, observed it to persist throughout. During the early stages of development spherical vessels of various sizes are present in large numbers within the egg. These globules are closely packed together, one above the other, and are very conspicuous in an egg eight days old (Pl. II. fig. 4). They appear to fill the egg, excepting for a small area round the periphery, which is occupied by a granuloid plasma containing many refractive particles. No cellular peripheral membrane was distinguishable in this egg. The chorion is conspicuous during the early stages of development, but as the egg increases in size it becomes thinner and more attenuated. As development proceeds, the egg gradually assumes a more or less oval shape, and the embryo may be discerned in the centre (Pl. II. fig. 6). The peripheral layer of cells constituting the embryonic membrane is now very distinct and lies immediately beneath the chorion. In a later stage the embryo becomes more clearly defined, lying in a curved position, and its cephalic region is very distinct (Pl. II. fig. 5). (This egg is actually younger than the egg (fig. 6), but its development nevertheless appears to be more advanced.) The embryo does not lie in contact with the embryonic membrane, but is separated from it by a clear space. If such an egg be removed to a slide and carefully dried it will retain its spherical shape, but if the chorion be pricked the egg collapses immediately and a mass of fluid exudes. The embryo must thus develop immersed in liquid, and it appears to maintain a central position in this fluid-filled sphere. As development proceeds, the space between the embryo and the embryonic membrane diminishes, as may be seen in Pl. II. fig. 7. In this specimen the segmentation of the body is complete, but the head is not chitinized and the mouth-parts are not distinguishable. As growth continues, the larva comes more closely into contact with the embryonic membrane, and, just before emergence is effected, this membrane has been found swathed closely round the larva and separated from the chorion in parts (Pl. III. fig. 1). In its final stages the so-called egg appears to superficial observation merely as a first stage larva surrounded by a cellular sac, and it is only by careful examination that the chorion may be distinguished as a thin transparent outer membrane. The extent to which the chorion may be stretched varies in different specimens.

In the egg figured (Pl. III. fig. 1) the larva has extended the chorion to 0·85 mm. long by 0·45 mm. broad. Some eggs in an earlier stage have been found with the chorion even further distended. In these cases the distension was not due to pressure by the embryo, which remained in the centre of the egg and was not in contact with the periphery One such egg measured without pedicel 0·88 mm. long by 0·72 mm. broad and another 0·9 mm. by 0·52 mm. Both contained embryos in an early stage of development like that figured in Pl. II. fig. 5. Such large eggs appear perfectly normal, and were obtained from healthy hosts. It is difficult to understand how the expansion of the chorion at this stage is effected. It seems probable that it is brought about by the growth of the cells of the embryonic membrane. The egg is immersed in the body-fluid of the host, and it seems impossible that the extension of the chorion could be caused merely by ingress of fluid into the already fluid-filled area round the embryo, but if a slight stretching of the chorion were occasioned by increase in the dimensions of the embryonic membrane, more fluid would enter accordingly. The increase in size of the egg during its development is thus enormous. The ovarian egg, as already stated, measures with pedicel 0·2 mm. to 0·24 mm. long by 0·036 mm. to 0·044 mm. broad across the middle. The pedicel itself is difficult to measure, as it grades imperceptibly into the egg, but it may be reckoned as from ·07 to ·08 mm. long, thus reducing the length of the egg to ·12 to ·17 mm. long. If these measurements be compared with the largest developed egg observed (0·9 mm. by 0·52 mm.) it will be seen that the egg during development attains 5 to 7 times its original length and about 12 to 14 times its width. A rough estimate has been made of the cubic contents of the egg at oviposition and when fully developed, and if the smallest ovarian egg be selected for comparison it is evident that the egg may increase its cubic content over twelve hundred times. This is probably a low estimate, as the ovarian egg tapers more at the extremities than the mature egg, and no allowance has been made for this. Oglobin (1913) also finds that the egg of *Dinocampus terminatus* (*coccinellæ*) enlarges one thousand times. The increase in size of the egg after oviposition has been observed in numerous endoparasitic Braconidæ, and is also known to occur in endoparasites of other Hymenopterous families: *e.g.*, in the Stephanidæ, as observed by Wardle (1914) in *Hypamblis*: in the Chalcid *Smicra* by Henneguy (1892); in the Proctotrypoid *Platygaster* by Marchal (1906), and doubtless in many other families.

Emergence of the Larva from the Egg.—Only in one instance has the act of eclosion been observed. An egg of *Dinocampus rutilus* containing a fully-developed larva had been dissected out of a weevil in a watch-glass under salt solution, and a sketch was being made of it with the aid of the camera lucida (Plate III. fig. 1). The larva, which was still alive, was lying in a wide semicircle, the head as usual at the cephalic pole of the egg and the caudal appendage bent between its body and the wall of the egg. The larva was completely swathed in the embryonic membrane. While watching the specimen through the microscope the larva was seen to straighten out its abdomen gradually; then quite suddenly with a vigorous movement, the posterior segments of the abdomen were straightened out, and at the same time the head and anterior segments of the body were shot forwards, bursting out of the chorion. The embryonic membrane still surrounded the larva like a complete and close fitting skin, and the chorion was left clinging to the posterior part of the body and drawn out into a point by the apex of the tail. The subsequent dissociation of the cells of the embryonic membrane will be described later. Once freed from this membrane the larva would have no difficulty in throwing off the chorion. Sometimes a larva has been observed with the chorion ruptured in two or more places, and in Pl. III. fig. 2 a larva has been figured in which the head and tail project at each end. It must be remembered that at this stage the chorion is much attenuated, and probably but little effort on the part of the larva is required to break it.

The emergence of the larva from the chorion by straightening the body has been observed by Strickland (1923) in *Meteorus dimidiatus* and Dustan (1921) in *Campoplex pilosulus*, and Muesebeck (1918) considers that one of the functions of the caudal appendage in *Meteorus versicolor* is to aid the larva in getting out of the egg.

The Embryonic Membrane.

Before Emergence of the Larva.—Since the embryology of *Dinocampus rutilus* has not been studied, the origin of the embryonic membrane has not been traced. It is conspicuous in eggs containing embryos of the stage figured on Pl. II. fig. 5, and forms a continuous membrane immediately beneath the chorion. It is made up of cells in which the nuclei are very distinct. In some specimens the cell-walls are more clearly visible than in others, and in Pl. IV. fig. 1 some cells have been drawn *in situ* with the camera lucida from the egg figured in Pl. II. fig. 6. The cells are very varied in size and shape. Some are more or less round, but the majority are pentagonal or hexagonal. In the egg figured in Pl. II. fig. 6, which was dissected from the host 27 to 33 days after oviposition, cells of the following sizes were common in the embryonic membrane: 48 μ by 24 μ; 44 μ by 40 μ; 36 μ by 28 μ; 36 μ by 20 μ; and 28 μ by 24 μ. The nuclei are slightly oval rather than spherical, and measure at this stage from 16 μ to 17 μ. An uneven sprinkling of highly refractive particles which are often of irregular shape is always present in the cytoplasm of the cells. By examining living eggs mounted in salt solution with a high power, it may be seen that these refractive particles consist of minute spherical droplets varying from about 1 μ to 3 μ in diameter. When two of these droplets lie close together they appear under lower magnification as a refractory particle of irregular shape. These minute globules occur in all parts of the cell, either above or below the nucleus, and they are often present in groups near the cell boundaries. They are not doubly refractive when examined with polarized light, and they stain readily with Sudan III. I have no doubt that these droplets consist of fat which the cells have absorbed from the body-fluid of the host. In addition to these globules, numbers of much larger vesicles are usually greatly in evidence, when one examines the embryonic membrane of a living egg of this stage. The nature of these vesicles is very difficult to ascertain. They vary greatly in size and abundance in different specimens, and may measure from 8 μ to 28 μ in diameter. They are faintly pink in colour, and may be spherical, oval, or even somewhat irregular in shape. In some specimens they are so numerous that they entirely obscure the nuclei and cell-walls. Since the chorion and the embryonic membrane are both so thin, the exact position of these vesicles is not easy to discover. In some specimens they appear to occur in a double layer, perhaps above and below the embryonic membrane. In other specimens, by careful focussing, they are seen to lie either on a level with the nuclei or slightly above or below them. They appear to be particularly abundant on the lower surface of the cells, but the fact that in some eggs they hide the cell-walls in surface view suggests that they occur also on the upper surface of this membrane and between it and the chorion. In some eggs they are to be found grouped in chains along the cell boundaries, and they are then usually of oval shape. In contrast to the small fat droplets already described, they do not stain at all in Sudan III. They are not doubly refractive in polarized light. They remained intact when the egg was fixed with Rippart and Petit's fluid. They did not stain with Methyl Green, but absorbed Eosin. They were not removed by treatment with 70 per cent. alcohol or warm water, but, after immersion of the egg in nearly boiling water, they mostly disappeared. Fixation with Flemming-without-Acetic caused the disappearance of all the vesicles which obscured the cell boundaries, but the sphericle vesicles, which appeared to occur within the cytoplasm of the cells, remained intact, though the fixative readily penetrated through the embryonic membrane to the embryo. When a portion of the membrane thus fixed was stained, dehydrated, and mounted, numbers of vacuoles were observed in the cells, but some of the smaller ones would doubtless be formed by dissolution of the small fat droplets. The possibility that these vesicles may be artifacts, produced by the action of the salt solution, cannot be ignored, but the fact that they vary so greatly in number and size in the different specimens, though examined in the same medium, is difficult to explain on this hypothesis. Moreover, the vesicles appear to be as prominent in eggs newly dissected from the host as in those which have been immersed over an hour in salt solution. While it is impossible from the present data to arrive at any definite conclusions in regard to the nature of these vesicles, it seems probable that they may represent dissolved nutritive matter derived from the body-fluid of the host. If this fluid were of a more viscid nature than the rest of the liquid within the egg, it would not merge with it at once, and so would remain visible as oily droplets. All the nutritive material required by the embryo must pass through the embryonic membrane. It may percolate principally through the boundaries of the cells, but it may perhaps also pass through the cytoplasm of the cells. Fixation with Flemming would serve to wash away all such substances present on the upper or under surface of the embryonic membrane, but if any vesicles were present within the cells they would remain undisturbed. It is possible that the nutritive fluids absorbed from the body-fluid of the host may undergo a further digestion in their passage through the cells of the embryonic membrane, and so reach the embryo in a condition more easy to assimilate. The embryo at this stage is undergoing rapid growth and development, and the nutritive matter is doubtless assimilated direct by the growing tissues from the liquid medium in which the embryo is immersed.

The cells of the embryonic membrane increase in size as the embryo develops. In an egg containing an embryo at a later stage of development than that of fig. 6 of Pl. II., the cells of the embryonic membrane (Pl. IV. fig. 3) measured 60 μ to 68 μ long by about 30 μ broad, and the nuclei were also larger (22 μ instead of 16 μ to 17 μ). Observations indicate that the cells attain nearly to their full size before the larva is completely formed, for, when the larva is ready to emerge from the chorion (some 20 days later), the cells were found to be of about the same size, but the nuclei were larger, measuring from 28 μ by 24 μ to 35 μ by 27 μ.

After the Emergence of the Larva.—When the larva ruptures the chorion to effect its emergence, it is usually more or less surrounded by the embryonic membrane. In some cases the larva doubtless breaks through the embryonic membrane in forcing its way out of the chorion ; and this appears to have happened in the case of the larva figured on Pl. III. fig. 2, where both chorion and embryonic membrane are rent at each end of the egg and the head and tail of the larva project free. At other times the larva may be completely surrounded by the membrane after breaking the chorion, and, while its own movements doubtless assist in freeing it, its liberation is invariably ensured by the dissociation of the cells of the embryonic membrane, which takes place at this time. In the larva figured (Pl. III. fig. 2), the embryonic membrane was found floating out behind it and was already commencing to break up. If the membrane at this stage be mounted in salt solution and examined under the high power, every stage in the process of dissociation may be traced. Thus it will be seen that in some places the membrane is intact, but in other places the cells composing it are commencing to dissociate. Such cells are assuming an oval instead of polygonal shape. They are still in contact with each other at the sides, but spaces may be observed between them in the corners originally filled by the angles of the cells (Pl. IV. fig. 4). Thus the cells soon become completely detached from each other, and may be found free in the body-cavity of the host. Sometimes small groups of cells become detached, but the individual cells separate later from each other. While still composing the embryonic membrane, these cells are transparent and flattened dorso-ventrally, and, when newly dissociated, they are oval in shape and somewhat flat. They soon, however, become completely spherical in form and of an opaque white colour. The nuclei of the cells about to dissociate show an increase in size, and in newly-separated cells measuring 60 μ by 49 μ the nucleus was observed to measure 37 μ to 40 μ. It is still distinctly visible by transmitted light appearing as a central zone of denser protoplasm. In the cytoplasm, numbers of small refractive particles occur, especially around the nucleus, but they are scarcer near the periphery. These particles are undoubtedly homologous with the minute fat droplets already described in the associated cells. They stain readily in Sudan III, and are not doubly refractile in polarized light. It is the abundance of these fat droplets that gives the cell its opaque white appearance. When cells which have been liberated for some time in the body-cavity of the host are examined in salt solution, transparent globules may be seen oozing from the periphery of each. These globules also stain with Sudan III., and are probably exudations of fatty matter.

Once free in the body-cavity of the host these cells do not perish, but maintain an independent existence. They increase greatly in size, and their development proceeds, as a rule, at the same rate as that of the larva, so that the size of the cells gives a rough indication of the size and age of the larva. Thus in winter, while the larva remains in the 1st instar for several months, the cells increase very little in size, but in summer, when the larval development is rapid, the dissociated cells develop accordingly. While there is this general uniformity in the growth of the cells, one never finds that all the cells are of exactly the same size at any one period. Thus a weevil which had been parasitized early in October was dissected in February, and was found to contain a single first instar larva, and the dissociated cells varied in size from 72 μ to 100 μ. It is probable that the small cells have developed more slowly, or they may have been smaller than the others before dissociation.

The cells appear as opaque white globules, and they are very conspicuous objects. They stream out into the dissecting dish the moment one ruptures the integument of the host, and their presence is always a sure indication that the beetle has been parasitized. The cells are to be found in numbers throughout the abdominal cavity of the host, and usually occur within the metathorax also. They are most numerous when the larva is young. Over 600 have been counted in one beetle containing a first instar larva, and 4217 in another host in which six first instar larvæ were present. It is probable that each egg gives rise to about 800 cells, but the exact number is not easy to ascertain, because, when newly dissociated, the cells are extremely small and difficult to count, and, as they become larger, they decrease in number. Observations indicate that the number of cells occurring in the embryonic membrane before dissociation is very high, and would more than account for the number of liberated cells present in the body-cavity of the host. Moreover, the cells have never been seen to divide after dissociation, and it is probable that the full number is present in the embryonic membrane some time before the larva emerges from the chorion.

As the cells increase in size the nuclei become of irregular shape, and are no longer easy to distinguish without sectioning the cell. In transmitted light the nucleus may just be distinguished as an ill-defined more or less square or star-shaped mass, and in sections it is seen to be very irregular in outline, indented or dumbbell-shaped. The cells ultimately attain a considerable size, measuring 220 μ to 350 μ. They now consist of little else but fat (Pl. IV. fig. 7), which is present in masses of minute globules 2 μ to 4 μ in diameter. The membrane of the cell has now become extremely stretched and thin. It ruptures with the least pressure and a cloudy effusion, composed of the minute fat droplets, pours out. Some of the cells were found to have a semi-transparent appearance, due to the fact that they had discharged some of their contents. Even the smaller cells present amongst the larger ones exhibit the same appearance and burst readily when pressed. When fixed with Flemming-without-Acetic and sectioned, the cells in these final stages show a ramified nucleus and the cytoplasm is packed with blackened granules of fat (Pl. IV. fig. 6). The effect of Osmic fixatives on the dissociated cells of different ages has been observed. The large cells fixed in Flemming frequently broke up when brought into 90 per cent. alcohol, and, while some of the fragments were seen to contain masses of black granules when mounted in Euparel, others were colourless, the osmicated fat having probably dissolved in the clearing reagent. Smaller and younger cells similarly fixed were mounted entire, but only the larger cells (168 μ) appeared brown, and this colour was confined to the central area of the cell and in some specimens subsequently disappeared. When the Flemming fixed cells were mounted in Glycerine without treatment with alcohol, the cells appeared brown, but this colour was due to the presence of masses of small globules 1·5 μ to 10 μ in diameter, the smaller ones being deep yellow and the larger ones tinged with brown. It was noticed that fragments of fat of *Sitona lineata* treated in the same way exhibited similarly coloured but slightly larger globules. The smaller and younger dissociated cells (32 μ to 64 μ) showed no blackening at all, even though fixed in Flemming for fourteen hours, but they exhibited masses of small yellow droplets. Fixed in Osmic acid the fat droplets of such cells appeared dark with low magnification, but under a higher power they were seen to be yellow, and, when mounted subsequently in Euparel, they showed no blackening. As has already been mentioned, the minute globules of the newly-dissociated cells stain strongly with Sudan III. and are not doubly refractive in polarized light. The globules occurring in the cells in their final stage behave in exactly the same way. There thus seems no reason to believe that the fatty matter present in these cells varies in constitution during the increase in size of the cell, and the failure to obtain the blackening reaction with the young cells after osmic fixatives probably indicates that sufficient fat is not present in the very small cells to produce this reaction, since the dark precipitate, even in the full-sized cells, is very readily dissolved.

As already mentioned, the dissociated cells of the embryonic membrane are most numerous during the early stages of parasitism when the larva is still in the first instar. It is in this instar that by far the longest part of the larval life is spent. During the later instars the larva increases rapidly in size, and it is during this period of active growth that the cells diminish markedly in number, and, by the time the larva leaves the host, the cells have all disappeared. Their fate is obvious, if one examines the gut of the larva. Within the mid-intestine of a nearly full-grown larva their remains are to be found in numbers, and, as will be shown in the second part of this paper, these cells undoubtedly constitute the principal food of the larva in its later stages. During the first instar comparatively few cells appear to be swallowed by the larva, and they are thus mostly spared to continue their function of storing up fat from the body-fluid of the host. They thus constitute a valuable food reserve, which is available to nourish the larva at the time when its growth is rapid. It has already been shown that the cells at this stage are much distended and easily ruptured, and this fact doubtless facilitates their consumption and digestion by the larva. It is probable that many of the cells at this stage get crushed by the movements of the larva within the host. Their fatty contents will in consequence be discharged into the body-fluid, and will thus be available also as food for the larva.

The cells of the embryonic membrane dissociate and continue their development even if the parasite larva dies before emerging from the egg. In the second part of this paper it will be shown that supernumerary larvæ frequently perish within the chorion. In such cases the cells of the embryonic membrane separate, assume a spherical shape, and become of the usual opaque white colour. They develop, in fact, just like the cells of a healthy larva, increasing in size, but they are imprisoned by the chorion, and are therefore forced to crowd into the fluid-filled space between the dead larva and the chorion. Such eggs are readily distinguishable from those containing living embryos by their peculiar opaque appearance. Occasionally these cells bring about an abnormal extension of the chorion. Thus, in one weevil which contained a living 2nd instar larva, an egg was found tightly packed with dissociated cells measuring 50 μ to 130 μ. The chorion had become so stretched that this "egg," an opaque white oval lump, measured 1·19 mm. by 0·73 mm. (The largest normal egg observed measured 0·9 mm. by 0·52 mm.) On opening the chorion the dissociated cells streamed out, and the dead larva was found within, shrivelled and contracted, measuring only 0·75 mm. In another case the cells had apparently, by their growth, caused the rupture of the chorion, for in one weevil containing a living 1st instar larva a disintegrated dead larva was found surrounded by the chorion, in which a hole occurred, and all but a few cells had come out by this hole into the body-cavity of the host.

In the instances just quoted several eggs had been laid in one host, and one larva remained alive, but it sometimes happens that the only larva present within a beetle may die while still young. In such cases also the cells of the embryonic membrane continue their development, and may even attain to an abnormal size. Thus in one instance a weevil which had been placed with a female Braconid for a few days in October was dissected the following April, no parasite larva having emerged in the interval. Numbers of comparatively large dissociated cells were found packed among the viscera in the body-cavity of the host, but at first I sought in vain for the parasite larva, which, judging from other breeding experiments and from the size of the dissociated cells, ought at least to have been in the 2nd instar. Eventually a small group of cells was found enclosed in the partially ruptured chorion of the Braconid egg, and, entangled in the chorion, was a dead 1st instar larva, already brown and partly decayed. The larva may perhaps have succeeded in breaking the chorion, or else the developing cells of the embryonic membrane may have burst it open. At the time of dissection the cells measured from 100 μ to 228 μ, and many of them were as large or larger than the head of the dead larva. About 450 were counted. In some cases it would appear that the larva may die at an earlier stage before it has developed its chitinous head-capsule. Thus in two instances many dissociated cells of unusually large size have been found in the body-cavity of a weevil, but most careful searching failed to reveal the presence of a larva. Doubtless the larva had died as an embryo and had disentegrated and left no trace. In the one host the cells measured from 200 μ to 580 μ, and about 150 were present. The weevil in this case had died, probably owing to the presence of so many large dissociated cells within its body. In the other weevil the cells were nearly as large. These cells, apart from their size, presented the same appearance as cells in a host containing a living larva, but they were less perfectly spherical in shape. They were found to rupture easily, discharging their fatty contents, which stained as usual with Sudan III. Doubtless these cells break down of their own accord when the cell membrane has been stretched to its extreme limit, and the friction of the cells amongst the viscera of the host would also tend to rupture the cell membranes. In this manner the cells would become reduced in numbers, and the occurrence of only 150 cells in the weevil mentioned above would be explicable.

On the Dissociation of the Embryonic Membrane in other Parasitic Hymenoptera.

The dissociation of the cells of the embryonic membrane would appear to be a phenomena of widespread occurrence amongst parasitic Hymenoptera. In many cases, however, the true nature of the liberated cells occurring within the body-cavity of the host has been overlooked. Thus one frequently finds descriptions of globules occurring in parasitized insects, but they have usually been mistaken for the disorganized fat-body of the host. I have no doubt that they represent, as in *Dinocampus*, the dissociated cells of the embryonic membrane. They have been observed by the following writers: Timberlake (1912) in *Limnerium validum*; Haviland (1921) in *Aphidius*; Speyer (1925) in *Perilitus melanopus*: Kaufmann (1923) in species of *Perilitus*; Oglobin (1913) in *Dinocampus terminatus* (*coccinellæ*); Seitner and Nötzl (1925) in *Cosmophorus henscheli*; Menzel (1926) in *Euphorus helopeltides*. Only in a few cases has the identity of these globules been recognized, and it is interesting to find that differences occur in their method of origin and in their subsequent development in the different species.

Henneguy (1904) has shown that in the Chalcid *Smicra* the amnion, which is derived by a simple delamination from the superficial cellular layer of the segmented egg, breaks up into its component cells some time before eclosion. These cells assume a more or less spherical form and commence to degenerate, their protoplasm becoming filled with fatty droplets. When the larva hatches, the cells are distributed in the body-cavity of the host, but it is not stated whether or not they subsequently increase in size.

Marchal (1906) gives a very interesting account of the dissociation of the embryonic membrane in the Platygasters. In *Trichacis remulus* the amnion is differentiated at the very beginning of segmentation. When the larva is set free in the body-cavity of the host, the amnion gives birth by dissociation to rounded or oval bodies which he terms "pseudogermes." Each of these bodies contains several nuclei, and becomes surrounded by an anhistous layer analogous to a chorion. The "pseudogermes" float in the blood of the host. They grow and multiply some time after their liberation. In the later stages of parasitism they become more and more transparent and the chromotin of the nuclei becomes weaker. A similar dissociation of the embryonic membrane was observed by Marchal in *Platygaster lineatus* and *P. marchali*. In *Platygaster ornatus* the development is rather different. The amniotic elements in this species are derived primarily from a single nucleus, the paranucleus, which, separated at an early stage of segmentation, becomes established in a layer of peripheral protoplasm distinct from the plasma of the cells of the embryo. The paranucleus increases in size and later undergoes a multiple division, giving rise to a crowd of small nuclei. These nuclei surround themselves with granular plasma and continue to multiply by direct division. At the same time the plasma which unites them grows and divides into irregular masses which Marchal terms "masses paraembryonnaires." When the larva becomes liberated in the body-cavity of the host, some of the paraembryonic masses remain attached to the larva, but others are set free and affect the form of "pseudogermes." Marchal describes this type of embryonic membrane as a "trophamnios."

In *Apanteles glomeratus*, Grandori (1911) observed that the amnion continues to encircle the larva throughout its life. It is at first a completely closed membrane, but later it exhibits many lacunæ, forming a sort of net round the larva. When the larva is mature the slender protoplasmic prolongations between the cells of the amnion dissolve, so that the cells become free from each other and are carried away in the circulating fluid of the host. They preserve their vitality to the end, and some may be found adhering to the body of the larva shortly before it leaves the host.

Spencer (1922) finds that, in the Braconids of the subfamily Aphidiinæ, the serosa breaks up into pieces at the time of hatching, each piece varying in size and number of nuclei. The fragments of serosa then round off and begin a strange process of vacuolization and growth. The nuclei, which enlarge also, break down and fuse, finally resulting in a shrunken mass of chromatin. The degenerate masses derived from the serosa are ultimately consumed by the larva at the time when it eats the internal organs of the host. In *Diæretus rapæ*, Spencer observed that the serosa was formed by delamination or extrusion of cells from the ectoderm of the embryo early in development.

It will thus be seen that the embryonic membrane does not always separate into its individual cells, as in *Dinocampus rutilus*, but may break up into pieces containing many nuclei. These pieces assume a spherical shape just as do the isolated cells. In this case, however, it is difficult to understand how the anhistous layer around the fragments described by Marchal is formed, for, in *Dinocampus rutilus*, the limiting membrane of the dissociated cell is, of course, the wall of the cell.

It is probable that in some cases, *e. g.* in that of *Apanteles*, the persistence of the cells of the embryonic membrane is of no value to the larva; but in *Dinocampus rutilus* I have no doubt that the curious development of these cells is of great importance to the larva, since they store up large quantities of fatty matter which is available for assimilation by the larva at a time when rapid growth is essential to it.

SUMMARY.

A review is given of the literature on the parasitism of Braconids of the genera *Dinocampus* and *Perilitus*. The records at present available show that these insects are parasites of beetles, usually of the adult insect, but occasionally of the larva also.

Dinocampus (*Perilitus*) *rutilus* is a parasite of adult weevils of *Sitona lineata*, and has also been obtained from *S. hispidula*.

This Braconid is common throughout the British Isles and is widely distributed in Europe.

Both sexes are equally numerous, but parthenogenesis may occur. Only males have been reared from unmated females.

The adult Braconids lived in captivity usually about a fortnight, but a few survived for three or four weeks.

The female effects oviposition in the apex of the abdomen of the host, pursuing the beetle assiduously until her task is accomplished.

The egg, when laid, is very small, but, after oviposition, the chorion expands and the egg enlarges to a remarkable degree, attaining to over a thousand times its original size.

During the development of the embryo a cellular membrane may be distinguished immediately beneath the chorion, and the cells of this membrane increase in size as the larva develops.

When fully formed, the larva ruptures the chorion and becomes free in the abdomen of the host.

At the same time the cells of the embryonic membrane commence to dissociate and to become dispersed throughout the body-cavity of the beetle.

They assume a globular form and become of an opaque white colour, due to the presence of fatty matter, which they absorb from the body-fluid of the host.

As the larva grows, the cells increase in size and their nuclei become of irregular shape.

In their later stages the cells of the embryonic membrane consist almost entirely of globules of a fatty nature. The membranes of the cells become much stretched and rupture with the least pressure, so that the fatty contents are discharged into the body-fluid of the beetle.

When the Braconid larva is young, as many as 600 or 700 dissociated cells of the embryonic membrane have been counted within the body of the host, but as the larva grows the cells diminish in number.

The dissociated cells of the embryonic membrane with their ingested fatty contents constitute the principal food of the larva in its later stages. Their remains may be found in numbers within the mid-gut of the full-grown larva.

If the parasite larva happens to die when still young, the cells of the embryonic membrane dissociate and continue to develop, sometimes attaining to an abnormally large size.

Comparatively few observations have been made in regard to the dissociation of the embryonic membrane in other parasitic Hymenoptera, and, while opaque white globules have been recorded as occurring in certain parasitized insects, they have usually been mistaken for "disorganised fat-body" of the host.

Bibliography.

Ashmead, W. H. 1886. "Description of New Braconidæ in the Collection of the U.S. National Museum." Proc. U.S. Nat. Mus. xi. pp. 611–671.

Balduf, W. V. 1926. "The Bionomics of *Dinocampus coccinellæ* Schrank." Ann. Ent. Soc. Amer. xix. pp. 465–498.

Bignell, G. C. 1891. Ent. Monthly Mag. p. 169.

Cameron, A. E. 1915. "Potato Spraying and Dusting in New Jersey, U.S.A." Bull. Ent. Research, vi. p. 19.

Chittenden, F. H., & Marsh, H. O. 1920. "The Western Cabbage Flea-Beetle." U.S. Dept. Agric. Washington, D.C., Bull. no. 902, 21 pp. (Abs. R. A. E. (A), ix. p. 203.)

Cushman, R. A. 1913. "Biological Notes on a few Rare or Little-known Parasitic Hymenoptera." Proc. Ent. Soc. Wash. xv. no. 4, pp. 153–160.

—— 1922. "The Identity of *Ichneumon coccinellæ* Schrank." Proc. Ent. Soc. Wash. xxiv. no. 9, pp. 241–242. (Abs. R. A. E. (A), xi. p. 117.)

Cutright, C. R. 1924. "Bionomics of *Hippodamia tredecimpunctata*." Ann. Ent. Soc. Amer. xvii. no. 2, pp. 188–192. (Abs. R. A. E. (A), xii. pp. 423.)

Doten, S. B. 1911. "Concerning the Relation of Food to Reproductive Activity and Longevity in certain Hymenopterous Parasites." Tech. Bull. 78, Agric. Expt. Sta. Univ. Nevada.

Dustan, A. G. 1921. "Some Notes on the Habits of *Campoplex pilosulus*, a Primary Parasite of the Fall Webworm." Proc. Ent. Soc. Nova Scotia, no. 6, pp. 81–88.

Elliott, E. A., & Morley, C. 1908. "On the Hymenopterous Parasites of Coleoptera." Trans. Ent. Soc. Lond. 1907, part 1, pp. 7–75.

Farrel, J. 1919. "Apple Culture in Victoria." Journ. Dept. Agric. Victoria, Melbourne, xvii. p. 31. (Abs. R. A. E. (A), ix. p. 8.)

Feytaud, J. 1917. "La Défense de la Vigne contre les Insectes." Bull. Soc. Étude, Vulg. Zool. Agric. Bordeaux, xvi. no. 5, pp. 33–42. (Abs. R. A. E. (A), v. p. 341.)

Genieys, P. 1925. "*Habrobracon brevicornis* Wesm." Ann. Ent. Soc. Amer. xviii. no. 2, pp. 143–202.

Glover, T. 1877. Ann. Rept. U.S. Dept. Agric. p. 99.

Grandori, R. 1911. "Contributo all' Embryologia e alla Biologia dell' *Apanteles glomeratus* (L.) Reinh." "Redia," Florence, vii. pp. 363–428.

Hallez, P. 1886. "Loi de l'Orientation de l'Embryon chez les Insects." C. R. Ac. Sc. Paris, ciii. pp. 606–608.

Hase, A. 1922. "Biologie der Schlupfwespe *Habrobracon brevicornis* (Wesmael). Braconidæ.' Arb. Biol. Reichsanst. Land- u. Forstw. xi. pt. 2, pp. 95–168.

Haviland, M. D. 1921. "On the Bionomics and Post-Embryonic Development of certain Cynipid Hyperparasites of Aphids." Q. J. M. S. lxv. pt. iii. pp. 451–478.

Henneguy, L. F. 1892. "Contribution a l'Embryogénie des Chalcidiens." C. P. Ac. Sc. Paris, cxiv. pp. 133–136.

—— 1904. Les Insectes. Paris, p. 337.

Hopkins, A. D. 1890. Insect Life, iii. no. 1, p. 20.

Hunter, S. J. 1909. "The Green Bug and its Enemies. A Study of Insect Parasitism." Bull. Univ. Kansas, ix. no. 2, 221 pp.

Jackson, D. J. 1920–22. "Bionomics of Weevils of the Genus *Sitona* injurious to Leguminous Crops in Britain." Ann. App. Biol. vii. pp. 18–298; ix. pp. 93–115.

—— 1924. "Insect Parasite of the Pea-Weevil." Nature, cxiii. no. 2836, pp. 353–354.

Kaufmann, Otto. 1923. "Beobachtungen und Versuche zur Frage der Ueberwinterung und Parasitierung von Oelfruchtsschädlingen aus den Gattungen *Meligethes*, *Phyllotreta*, *Psylloides* und *Ceuthorrhynchus*." Arb. Biol. Reichsanst. Land- u. Forstw. xii. no. 3, pp. 109–169. (Abs. R. A. E. (A), xii. p. 26.)

Kunckel d'Herculais, J., & Langlois, C. 1891. "Mœurs et Métamorphoses de *Perilitus brevicollis* Haliday." Ann. Soc. Ent. France, Séance du 27 Mai, 1891, lx. pp. 456–466.

Lean, O. B. 1926. "Observations on the Life-History of *Helopeltis* on Cotton in Southern Nigeria." Bull. Ent. Research, xvi. pt. 4, pp. 319–324.

Lesne, P. 1892. Ann. Soc. Ent. Fr. lxi. pp. 305–308.

Lichtenstein, J. L., & Picard, F. 1918. "Étude Morphologique et Biologique du *Sycosoter lavagnei* Picard et J. L. Licht. Hecabolide Parasite de l'*Hypoborus ficus* Er." Bull. Biol. France et Belgique, Paris, li. pp. 440–474.

McColloch, J. W. 1918. "Notes on False Wireworms, with especial reference to *Eleodes tricostata* Say." Journ. Econ. Entom., Concord, xi pp. 212–224. (Abs. R. A. E. (A), vi. p. 308.)

—— 1919. "*Eleodes opaca* Say, an Important Enemy of Wheat in the Great Plains Area." Journ. Econ. Entom., Concord, xii. no. 2, p. 190. (Abs. R. A. E. (A), vii. p. 282.)

Marchal, P. 1906. "Recherches sur la Biologie et le Développement des Hyménoptères Parasites." Arch. Zool. Exp. et Gen., IV^e Serie, iv. pp. 485–640.

Marshall, T. A. (A) 1885–1899. "Monograph of British Braconidæ." Trans. Ent. Soc. Lond. 1885, 1887, 1889, 1891, 1894, 1895, 1897, 1899. 8 pts

—— (B) 1891. "Les Braconides." v. pp. 45 46 of André's 'Species des Hyménoptères d'Europe and d'Algérie.' Paris.

Menzel, R. 1926. "Ueber Teeschädlinge in Niederländisch-Indien und ihre Bekämpfung. *Euphorus helopeltidis* Ferrière (Hym. Braconidæ) als Larven parasit der Tee-Capside *Helopeltis antonii* Sign." Zeitschr. angew. Ent., Berlin, xii. no. 2, pp. 340–356.

Moore, B. A. 1913–14. "The Wheat-Louse, *Toxoptera graminum*." Agric. Journ. Union S. Africa, Pretoria. (Abs. R. A. E. (A), ii. p. 154.)

Muesebeck, C. F. W. 1918. "Two Important Introduced Parasites of the Brown-Tail Moth." Journ. Agric. Res. Washington, D.C. xiv. no. 5, pp. 191–206.

Ogloblin, A. 1913. "On the Biology of Coccinellids (Russ.)." Revue Russe d'Entomologie, St. Petersburg, xiii. no. 1, pp. 27–43. (Abs. R. A. E. (A), i. pp. 457–458.)

Pennington, W. E. 1916. "Notes on *Rhogas terminatus* Cress." Journ. Econ. Entom. Concord. ix. pp. 401–406.

Picard, F. 1913. "La Lutte contre l'Altise dans l'Herault." Bull. Agric. d'Algérie et de la Tunisie, no. 4, pp. 86–89. (Abs. R. A. E. (A), i. p. 173.)

Ratzeburg, J. T. C. 1852. 'Die Ichneumonen der Forstinsekten,' iii. p. 61.

Riley, C. V. 1888–9. Insect Life. i. no. 4, pp. 101–104, & no. 11, pp. 338–39.

Ruschka, F. 1925. "Beitrage zur Kenntniss der forstlichen Braconiden." Zeitschr. angew. Ent. xi. no. 2, pp. 197–202.

Seitner, M., & Nötzl, P. 1925. "*Pityophthorus henscheli* Seitner, und sein Parasit, *Cosmophorus henscheli* Ruschka." Zeitschr. angew. Ent., Berlin, xi. no. 2, pp. 187–196.

Shevirev, I. J. (A) 1913. "The Regulation of Sex of their Offspring by Female Ichneumonidæ." (Russ.) Bull. du Laboratoire Biologique de St. Petersburg, iii. no. 2, pp. 24–30. (Abs. R. A. E. (A), ii. p. 214.)

Shevirev, I. J. (B) 1913. "La rôle des femelles dans la détermination du sexe de leur descendance dans le groupe des Ichneumonides." Comptes Rendus Hebdomadaires de la Soc. de Biologie, Paris, i. pp. 698–699.

Shtcherbakov, Th. 1916. South Russian Agric. Gazette, Charkov, xviii. (Abs. R. A. E. (A), v. p. 89.)

Sichel, J. 1854. Bull. Soc. Entom. France, 3rd series, ii. p. lvii.

Spencer, H. 1922. "Biology of the Parasites and Hyperparasites of Aphids." Ann. Ent. Soc. Amer. xix. pp. 119–157.

Speyer, W. 1921. "Beiträge zur Biologie des gefleckten Kohltriebrüsslers (*Ceuthorrhynchus quadridens* Panz.)." Entom. Blätter, xvii. pp. 118–124.

—— 1925. "*Perilitus melanopus* Ruthe als Imaginal parasit von *Ceuthorrhynchus quadridens* Panz." Zeitschr. angew. Ent., Berlin, xi. no. 1, pp. 132–146.

Strickland, E. H. 1923. "Biological Notes on Parasites of Prairie Cutworms." Can. Dept. Agric. Bull. no. 26. (Entom. Bull. no. 22, 40 pp.)

Swenk, M. H. 1923. "The Plains False Wireworm and its Control." Nebraska Agric. Exp. Sta. Circ. xx., 11 pp. (Abs. R. A. E. (A), xi. p. 449.)

Szépligeti, Gr. V. 1904. "Hymenoptera, Fam. Braconidæ." Fasc. 22, Wytsman's Genera Insectorum, pp. 174–175.

Timberlake, P. H. 1912. "Experimental Parasitism. A Study of the Biology of *Limnerium validum* (Cresson)." U.S. Dept. Agric. Bur. Ent., Tech. Ser. no. 19, pt. v. pp. 71–92.

—— 1916. "Note on an Interesting Case of two Generations of a Parasite reared from the same Individual Host." Canad. Entom. London, Ontario, xlviii. pp. 89–91.

—— 1917. "Notes on Some of the Immigrant Parasitic Hymenoptera of the Hawaiian Islands." Proc. Hawaiian Ent. Soc. Honolulu, iii. no. 5, pp. 399–404. (Abs. R. A. E. (A), vi. p. 352.)

Tower, D. G. 1915. "Biology of *Apanteles militaris*." Journ. Agric. Res. Washington, D.C. v. no. 12, pp. 495–507.

Tullgren, A. 1916. "En lömsk fiende till vår vän nyckelpigän." Entomologisk Tidskrift (Stockholm), pp. 95–98.

Viereck, H. L. 1913. Proc. U.S. Nat. Mus. xliv. p. 561.

Wade, J. S., & Boving, A. G. 1921. "Biology of *Embaphion muricatum*." Journ. Agric. Res. Washington, D.C. xxii. no 6, pp. 323–334. (Abs. R. A. E. (A), x. p. 112.)

Wardle, R. A. 1914. "Preliminary Observations upon the Life-histories of *Zenillia pecops* B. & B. and *Hypamblis albopictus* Grav." Journ. Econ. Biol. ix. no. 3, pp. 88–104.

Webster, F. M. 1909. "Investigations of *Toxoptera graminum* and its Parasites." Ann. Ent. Soc. Amer. ii. no. 2, pp. 67–86.

Weed, C. M., & Hart, C. A. 1889. "Notes on the Parasite of the Spotted Lady Beetle, *Megilla maculata*." Psyche, v. no. 156, pp. 188–190.

Westwood, J. O. 1840. An Introduction to the Modern Classification of Insects, ii. p. 142. London.

Willard, H. F. 1920. "*Opius fletcheri* as a Parasite of the Melon-Fly in Hawaii." Journ. Agric. Res. Washington, D.C. xx. no. 6, pp. 423–438.

EXPLANATION OF THE PLATES.

Plate I.

Dinocampus (Perilitus) rutilus Nees. Female × 22.

Plate II.

Eggs of the autumn generation of *Dinocampus (Perilitus) rutilus* Nees, showing stages in development. The drawings have been made from living specimens examined in salt solution.

Fig. 1. Optical section of ovarian egg at an early stage, surrounded by sheath of follicle cells and still attached to the vitellogenous cell. × 135.

Fig. 2. Optical section of fully-formed ovarian egg in sheath of follicle cells. × 185.
Fig. 3. Ovarian egg ready to be laid. × 81.
Fig. 4. Optical section of egg from an unmated female dissected from host 8 days after oviposition. × 81.
Fig. 5. Egg from female (probably fertilized) dissected from host about 20 days after oviposition. (The chorion and embryonic membrane are figured in optical section.) × 81.
Fig. 6. Egg from unmated female dissected from host 27 to 33 days after oviposition. Surface view showing cells of embryonic membrane as seen through chorion. × 81.
Fig. 7. Egg from female (probably fertilized) dissected from host 39 days after oviposition. (Chorion and embryonic membrane seen in optical section.) × 81.

PLATE III.

Fig. 1. Egg from unmated female of *D. rutilus* with full-grown larva ready to emerge. Dissected from host 51 to 55 days after oviposition. The caudal appendage of the larva is bent beneath its body and does not show in this figure. × 75.
Fig. 2. Larva of *D. rutilus* emerging from chorion. × 62. The egg had been laid from 50 to 54 days previously.

Both figures have been drawn from living specimens examined in salt solution.

PLATE IV.

Cells of the embryonic membrane of *D. rutilus* in various stages of development. With the exception of fig. 6, all the drawings have been made from specimens examined in salt solution. All magnified 250 times.

Fig. 1. Portion of embryonic membrane of egg figured Pl. II. fig. 6. Seen *in situ* through chorion.
Fig. 2. Surface view of portion of egg laid by unmated female dissected from host 45 to 47 days after oviposition. The cells of the embryonic membrane cannot be distinguished as they are obscured by the numerous vesicles.
Fig. 3. Portion of embryonic membrane of egg 28 to 29 days after oviposition. Seen *in situ* through chorion.
Fig. 4. Portion of embryonic membrane figured while still partially surrounding the larva after its emergence from the chorion, and showing some of the cells commencing to dissociate. From an egg laid 54 days previously.
Fig. 5. A & B. Completely dissociated cells from the embryonic membrane of the same larva. C. Dissociated cell, later stage, surface view, showing fat droplets.
Fig. 6. Section of dissociated embryonic cell in its final stage, fixed in Flemming-without-Acetic, stained Ehrlich's Hæmatoxylin and Eosin.
Fig. 7. Dissociated embryonic cell in its final stage, showing fat globules oozing out at periphery.

Explanation of Lettering.

C.	Chorion.
CE.	Cells of embryonic membrane.
EM.	Embryonic membrane.
F.	Cells of follicle.
G. I. & G.III.	Nerve ganglia of 1st and 3rd post-cephalic segments of larva.
GV.	Germinal vesicle.
P.	Pedicel.
RP.	Refractive particles.
RV.	Remains of vitellogenous cell.
VC.	Vitellogenous cell.
VS.	Vesicle.
X.	Cells of embryonic membrane completely united.
Z.	Cells of embryonic membrane commencing to dissociate.

23. Hints on the Transport of Animals. By Major STANLEY SMYTH FLOWER, O.B.E., V.P.Z.S., and others*†.

[Received June 13, 1928: to be Read October 22, 1928.]

INTRODUCTION.

The following letter, addressed by the Secretary of the Zoological Society of London to Major Stanley Smyth Flower, a Vice-President of the Zoological Society of London, and for many years Director of the Zoological Gardens at Giza, Cairo, explains the origin of this paper:—

Zoological Society of London,
November 29th, 1927.

MY DEAR FLOWER,

TRANSPORT OF ANIMALS COMMITTEE.

You have kindly agreed to be Chairman of what for short we may call the Transport of Animals Committee.

There is a considerable transport of living mammals, birds, reptiles, amphibia, and fishes, some consigned directly to Zoological Gardens, others to amateurs, others to the trade for sale. In our experience here, the incidence of mortality on new arrivals is out of proportion to the natural viability of the animals concerned and points directly to the operation of factors which might be eliminated. Purchasers from dealers have similar experience. This summer Mr. D. A. Bannerman and Mr. Norman Kinnear called my attention to specific instances of transport under extremely unsuitable conditions, and asked if some steps could not be taken. I replied that in my opinion the fault was largely due to ignorance and that the Zoological Society had always found prospective donors very ready to accept suggestions as to suitable cages, food for the voyage and so forth, and that information of that kind might be extended and put in suitable form for distribution. I undertook to bring the matter before the Council of the Zoological Society together with the suggestion that a Committee might be appointed to draft suitable instructions.

---

* This paper is based on the work of a Committee appointed by the Zoological Society of London, and consisting of Major S. S. Flower, Chairman; D. A. Bannerman; E. G. Boulenger, F.Z.S., Director of the Aquarium; G. B. Chapman, F.Z.S.; F. N. Grosvenor, P. & O. and Allied Lines; P. J. L. Kelland, Deputy Chief Veterinary Officer, Ministry of Agriculture and Fisheries; Miss E. Maud Knobel, F.Z.S.; Miss Joan B. Procter, F.L.S., F.Z.S.. Curator of Reptiles; D. Seth-Smith, F.Z.S., Curator of Mammals and Birds; Colonel A. K. Wyllie, Royal Society for Prevention of Cruelty to Animals. It contains Practical Advice on the Selection, Packing, and Hygiene of living Mammals, Birds, Reptiles, Amphibia, and Fishes for Transport by Sea and Land.

† Copies of this paper, in pamphlet form, may be obtained from the Secretary, price 6*d*. each, or 50 copies for £1.

The Council accepted the suggestion and appointed the following Committee, requesting you to act as Chairman:—

Major Stanley Flower, O.B.E., F.L.S., Vice-Pres.Z.S.
Mr. D. Seth-Smith, F.Z.S., Curator of Mammals and Birds.
Miss Joan B. Procter, F.L.S., F.Z.S., Curator of Reptiles.
Mr. E. G. Boulenger, F.Z.S., Director of the Aquarium.

They also asked me to invite in their name a representative dealer to serve, and to ask various other authorities to nominate members. The Committee, therefore, has been strengthened by the addition of the following:—

Mr. G. B. Chapman, F.Z.S., a large importer of animals.
Mr. Norman Boyd Kinnear, F.Z.S., nominated by the Trustees of the British Museum.
Mr. D. A. Bannerman, nominated by the British Ornithologists' Union.
Miss E. Maud Knobel, F.Z.S., nominated by the Avicultural Society.
Colonel A. K. Wyllie, nominated by the Royal Society for the Prevention of Cruelty to Animals.
Mr. P. J. L. Kelland, Deputy Chief Veterinary Officer, nominated by the Ministry of Agriculture and Fisheries.
Mr. F. N. Grosvenor, representing the P. & O. and Allied Lines.

The Home Office express sympathy with the objects of the Committee, and the Mercantile Marine Department of the Board of Trade offer any information or assistance they can in regard to the physical means of conveyance of animals on board ship. They also offer to send representatives with experience to meet the Committee after suitable conditions have been formulated for different kinds of animals.

I myself, Dr. G. M. Vevers, Superintendent of the Gardens, and Dr. H. H. Scott will be most ready to give you any assistance or information in our power.

The Council of the Zoological Society did not draft a formal reference, preferring to give the Committee as free a hand as possible. In a general way your function is consideration of all stages in the transport of animals from the selection of suitable individuals for travelling to their first care after unpacking at their ultimate destination. This will include:—

Simple criteria of health and condition before packing.
Securing that selected animals are willing to take the food which can be supplied them during transport.
Suitable boxes, cages, and packing.
Directions for hygiene during transport.
Food-supply during transport.
Attention required during transport.
Immediate treatment on reception.
Temporary detention pending ultimate destination.

As you personally have much experience in the transport of animals, I need not remind you of the need of attention to such points as the relative size of packages and cages, the numbers in each cage, provision for feeding, watering, and cleaning (in particular the avoidance of cleaning with salt water at sea), prevention of teasing or injudicious feeding by unauthorised persons, ventilation and freedom from draught, suitable temperatures, prompt removal of unused food, and so forth.

It has also to be kept in mind that the conditions suggested often will have to be carried out in remote parts of the tropics or in ports where makeshift devices alone are possible.

It is the hope of the Council that you will be able to draw up, so to speak, specifications for a large number of different kinds of animals. If you succeed in this I shall be glad of the suggestions and advice of the Committee as to the best form in which your recommendations might be published, as, for example, in a number of pamphlets.

It also may be possible, and on this I shall be glad of the advice of the Committee, that we should approach Shipping Companies with the view to their favouring shippers who comply with the suggestions you lay down, and with Insurance Companies to the same effect.

May I add that the Council of the Zoological Society attaches great hopes to the results of your deliberations, and that if in the course of your enquiry you find that there is any assistance we might be able to give you, we shall do our best to comply with your request.

Believe me,

Yours very sincerely,

P. Chalmers Mitchell.

The Committee held a number of Meetings, some in full session, others divided into sub-committees for different parts of the work, took evidence from a number of persons, and finally reported to the Council of the Society unanimously. The recommendations and advice which follow are based on their labours, and are recommended to all who have any concern with the transport of living animals.

P. Chalmers Mitchell,
Sec. Zool. Soc.
S. S. Flower,
V.-P. Zool. Soc.

General.

Some of the suffering and loss amongst birds and mammals during transport to Great Britain is indirectly due to excessive charges for freight and dock dues, out of all proportion to the charges on ordinary merchandise. This leads the importer to conserve his space to the utmost with the result of overcrowding.

Serious mortality is due to transhipment. Many of the British Shipping Lines decline to carry live stock, except at prohibitive rates, necessitating their being shipped by foreign lines to some continental port, whence they have to be transhipped by a Channel steamer which often has no suitable accommodation. The stock is consequently placed on deck and suffers much from exposure.

It would be to the advantage of the animals that they should be carried by Lines direct to their ultimate Port, thereby avoiding transhipment delay and discomfort. Importers doubtless are prepared to pay a remunerative freight, and would gain by less mortality and the better condition of their stock on arrival.

WATERING.

No hard and fast rules can be made on this subject. There are two main considerations.

(1) *Water, Available supply of, and its quality.*—Large ocean-going modern steamships may have a liberal supply of good fresh water, but on sailing ships, coast, and especially river steamers the supply of water available for animals may be very limited and so must be used as economically as possible. River-water may be brackish, or full of mud and other worse impurities. On long train journeys in the tropics water for animals may also be the chief anxiety: well-water, as used for the engines, may be charged with various salts which may have bad effects on thirsty animals if they are allowed to drink it.

(2) *Water, Animals' need of.*—This varies to an extraordinary extent both by species, by individuals, and by the humidity of the air. To take an extreme example—a one-humped camel before embarkation can be trained to drink once every six days, so on board ship every sixth day he should be encouraged to drink his fill, and given no water at any other time. Many gazelles, and other antelopes, only require water once in three days, and some of the African carnivora, as well as other mammals, at most once a day. In transit the actual amount of watering must be at the discretion of the attendant. It is no good putting water into the box, where it may be splashed about and wasted. The attendant must wait patiently to see what each animal actually drinks. Few things tend more to make a wild animal become tame and friendly than the manner in which it is watered.

(3) *Watering Monkeys.*—Water placed in a pan, or other vessel, in a monkey's cage in transit may be spilt, wasted, or fouled. Monkeys, Asiatic or African, can be easily trained to drink from the spout of a water-can. The attendant should, with a water-can full of water in his hand, place the spout through the bars or wire of the travelling-box and allow each monkey to drink its fill from the spout; no water will thus be wasted or

splashed about the box or deck. When several monkeys are in one box they quickly learn to drink in turn, and this gives the attendant good opportunities of getting to know them individually and studying their particular needs.

SHAPE OF BOXES.

(1) "Square" boxes are the least desirable for the transport of most animals (mammals, birds, or reptiles).

An oblong box should be used: for example, a box 2 feet square takes up 8 cubic feet of room, a box 1 foot wide by 2 feet high by 3 feet long takes up 6 cubic feet and is preferable in other ways.

In an oblong box an animal (when the box is shaken in handling, or by the motion of a ship, etc.) has the chance of "bracing" itself against the sides on the shorter axis, which it will quickly learn to do. In a square box the animal may slide from side to side till it gives up attempting to help itself.

There is also the advantage that the animal can retire from the door of the box (the door should be at one end) if it wishes, and so gets better privacy and a sense of security. Actually it is best to have a door at each end of the box, one for regular use and one for special occasions, such as catching the animal for examination by hand or for transference to another box.

As every traveller knows, "square" boxes are the most difficult to handle. Oblong boxes are easier to lift by hand, to transport by donkeys, mule, camel, or motor-cars, and to stack in railway carriages, cabins, etc.

(2) "Separate sleeping compartment" for monkeys, small cats, mongooses, squirrels, etc.

It is often more convenient to have this on the top of, instead of at the back of, the main compartment. All that is required is to have an oblong box stood on end, with, of course, suitable doors, so as to make a two-storey cage with a sliding door in the floor of the second storey.

CONSTRUCTION OF BOXES.

(1) *Bars or Wire.*

Iron bars may be difficult to obtain, and require a skilled artisan to place in position. One single bar displaced may lead to a disaster.

Galvanized wire netting, of various strengths and size of mesh, can be conveniently carried in short lengths in rolls. With unskilled labour a wooden frame, or an otherwise weak wooden box, can be quickly transformed into a strong cage by winding the wire once or twice round it, in one or two directions.

(2) *Metal-lined Boxes.*

Metal linings require skilled artisans to be effective, and a loose corner or turned-up edge may lead to the undoing of the whole structure in the hands of a persevering bear.

A box constructed of good hard wood with smooth interior surfaces is preferable for dogs, hyænas, etc. to a metal-lined box. *Some* porcupines will in time eat through any wooden box, but some will travel safely in a wooden box wrapped in wire.

(3) A flap of canvas or sacking should be provided to let down over the fronts of all cages or boxes for mammals and birds. This keeps the occupants quiet, cool in warm weather, and freer from draught. It also prevents them from being frightened by people passing.

(4) The most convenient doors for cages and boxes are those sliding vertically (made loosely in case the wood swells). They lessen the risk of escapes, as they can be opened just enough to admit the hand or the food and water dishes, and they close automatically. Two doors, placed at different sides so that every part of the interior can be reached, are useful.

VERMIN.

Before shipping animals, patient effort should be made to get them tame enough to be handled by the man, or men, who look after them, so that once the animals are used to being handled they may be searched for such vermin as ticks that can be picked off by hand.

Most wild animals in a state of nature seem to carry on their skins a large population of ticks, fleas, and lice. It is difficult to remove these from a frightened nervous beast, but in the case of a young animal, whether lion or buffalo, that is used to and fond of being handled, most of this vermin can be removed with care and patience: ticks by hand-picking, fleas by rubbing in Keating's Powder, and lice by fine-combing and a veterinary lamp.

Tortoises, snakes, and other reptiles often require de-ticking before shipment. (See special directions in Reptile Section, p. 649.)

PROTECTION FROM WEATHER, ETC.

When at sea, the ship's officers can generally be relied on to see that animal passengers are given all possible protection from sun, wind, and rain.

The danger times for animals in transit are in ports, railway stations, etc., where the boxes may get left for hours on a quay or a platform, under a very hot sun or in a biting wind, etc. It is then particularly that there must be an attendant with them, with a supply of suitable tarpaulins, blankets, ropes, etc., to be able to rig up such temporary shelter as may be required.*

Animals in cages also run more risk of being teased and baited by human beings when on shore than when on board ship.

On board ship cleaning must be undertaken thoroughly and regularly, at least once a day. The butcher is the official in charge of all pets and animals, and it is wise for the passenger who may be accompanying the animals to discuss, at the beginning of the voyage, the feeding and cleaning, and to find out at what time it is convenient for the butcher to help daily with these operations. This is the more useful, as he can easily obtain the food required from the ship's stores, and also pails, sponges, fresh water, etc. Before shipping a list should be prepared, giving under the number stencilled on the boxes or cages, the number of creatures in each and the food required for each. A copy of this list should be given to the butcher. It is also useful to make friends with the chief officer, the boatswain, and the chief steward, as the two former can do much by having screens rigged up, moving the boxes or cages to suitable places according to the weather, whilst the latter can supply delicacies otherwise not obtainable.

MAMMALS.

All animals should be kept in captivity before shipment long enough to enable them to become accustomed to human beings and to the kind of food that can be supplied to them during the voyage.

No young animal that is not thoroughly weaned, nor any female known to be advanced in pregnancy should be shipped, and great care must be taken that all animals are in good health and condition.

Stags should be shipped only when their horns are hard, and these should be sawn off before boxing.

In the case of animals larger than a squirrel it is desirable, wherever possible, that a Veterinary certificate as to the health of each animal, and its ability to stand the voyage, be obtained before shipment. Failing such expert opinion, there should be a statement signed by some responsible person that the animals appeared to be sound, undamaged, and in good health and were taking their food well.

BOXING *.

Zebras, *Antelopes*, *Deer*, *etc.* — Strong boxes are necessary, sufficiently large for the animals to stand and lie down, but not large enough to enable them to turn round, care being taken to avoid projections of any kind inside the box. The roof of the box should be 6 inches above the head of the animal and the box be 18 inches longer than the animal's greatest length. The whole of the back of the box should form a slide to draw right out at the top and on the top or roof of the box it is necessary to have a hinged flap, some 6 inches wide, which will lift up and allow the slide to be drawn out. It is essential that boxes be padded to prevent chafing. This padding ought not to be less than 12 inches deep, and run from the point of the animal's shoulder along either side to the back, the centre being at shoulder-level. It is necessary also for the slide at the back to be padded to within a foot of the top and the bottom.

---

* See also general notes on this subject.

Padding should be of strong canvas or hessian stuffed with soft material, such as shavings or fibre, but *not hay or straw* (the importation of which is prohibited by the Ministry of Agriculture), and fastened on with staples or clout-nails, the lower edge being turned in so that the nails or staples are covered by the canvas.

The top of the front for some 18 inches should be of wooden bars and have an opening 12 inches deep with hinged flap to allow for feeding and watering.

Provision must be made for feeding from the front by means of a manger fastened just inside the front by hooks. Mangers to be made movable and interchangeable with metal-lined drinking receptacles. The manger should be at the level of the animal's chest.

Narrow battens of hard wood should be screwed transversely across the floor of the box to prevent slipping, the screws to be well countersunk, and holes bored in the floor for drainage.

For cleaning out the box it is necessary to have a hinged opening, secured with buttons, at the bottom of the slide in the rear of the box.

Lions and Tigers.—For these animals the size of the box required is about 6 feet long, 2 feet 6 inches wide, and 4 feet high, very strongly built of hard wood, with one end formed of strong iron bars of 1 inch diameter and 3 inches apart in the clear, let into an iron frame forming a sliding door. A space of 3 inches to be left at the bottom for cleaning, feeding, and watering. The sides should project some 4 inches beyond the bars, to allow of shutters of close-fitting boards being fitted, leaving a space of some 3 inches between the bars and the shutters. Holes must be bored in the shutters for ventilation. Such boxes require to be well made by experienced carpenters.

Leopards, Pumas, and the medium-sized Cats.—Similar boxes but proportionately smaller, with the bars about 2 inches apart.

Wolves and Hyenas and Wild Dogs.—Similar boxes as for Leopards, etc., but metal-lined, if really hard wood is not available.

Bears.—Bears are usually imported when young and of small size. If adult they require a similar box to that used for a Lion, but it must be lined with sheet-iron. Young animals need proportionately smaller boxes.

Foxes, Small Cats, Mongooses, Martens, Opossums, etc.—A suitable sized box for each animal would be about 3 feet to 3 feet 6 inches by 1 foot to 1 foot 6 inches wide, which will allow plenty of room to turn round in; a separate sleeping compartment should be provided.

Wombats, Porcupines, and other Gnawing Animals require boxes lined with metal. A box of 3 feet 6 inches by 2 feet by 2 feet would be suitable for an adult Wombat or Porcupine.

The Smaller Rodents require metal-lined boxes in which they can move about freely, but with wire-netting instead of iron bars. A separate sleeping compartment should always be provided and a canvas flap to let down over the front.

Kangaroos.—Oblong boxes are most suitable, varying from 3 feet to 4 feet 6 inches in length, according to the size of the animal. They should be of light wood, close-boarded, the front closed halfway up, and the top half formed of wooden bars, with a narrow opening at the top of the back of the box, covered with wire-netting for ventilation. It is necessary to have a door in the lower half of the front, and a canvas flap must be provided for letting down over the front. Receptacles for food and water should be about 8 inches square.

Anthropoid Apes.—These should only be imported by individuals who are prepared to give them constant personal attention. They require to sleep in warm boxes with blankets or other coverings, and often pine and die unless they have the companionship of human beings or others of their own species.

Adult Anthropoids of the larger species require very strong boxes with iron bars and sufficiently large to enable them to stand upright comfortably and move freely. The importation of any adult wild-caught Gorillas or Orangs is to be discouraged.

Single Monkeys and Lemurs, or Pairs.—These require box-cages with strong wire netting, or wooden or iron bars in front, and with a bench at the back some 8 inches from the bottom. There should be a space of 2 inches at the bottom for cleaning, with a hinged flap, and a door in front for feeding and watering. A box of 1 foot 6 inches by 1 foot 6 inches by 2 feet high, provided with a canvas flap to let down over the front, is suitable for a small Monkey.

Baboons and other Large Monkeys with Short Tails.—Similar boxes, proportionately larger, are suitable.

Langurs and other Long tailed Monkeys.—Higher boxes in which the shelf can be fixed not less than 18 inches from the ground are necessary.

South American Monkeys (including Marmosets).—Boxes for these Monkeys should be provided with sleeping compartments on a shelf or above, and they travel best when several individuals are placed in the same box. A box 2 feet by 1 foot would be suitable for six or eight Marmosets or a pair of Squirrel Monkeys.

NOTE.—Young Rhesus Monkeys are imported from Calcutta in boxes 48 inches by 30 inches by 21 inches—not more than twenty in a box. These boxes have slatted bottoms, leaving a space of about 2 inches between this and the solid wooden bottom for cleaning purposes, the front, and a narrow strip about 1 inch deep at the top of the back, being wired. There is a considerable trade in these Monkeys, and the Sub-Committee inspected some of these cases containing Monkeys arriving from India, and considered them suitable for their purpose.

NOTE.—The recommendations under this heading refer mostly to single animals, and the desirability, or otherwise, of carrying more than one animal in the same box is a matter for the judgment of the individual shipper.

NOTE.—All boxes which are liable to stand on deck should be provided with feet or battens to allow of a space of 3 or 4 inches between the bottom of the box and the deck.

NOTE.—In the case of all heavy boxes handrails for lifting should be securely bolted to the sides.

NOTE.—The importation of such animals as Elephants, Hippopotamus, Rhinoceros, Giraffes, Swine, and Ant-eaters is not specially dealt with here, as they are rarely imported and each case requires special arrangements.

FOOD.

General.—An ample supply of food and bedding for the voyage must be placed on board at the port of embarkation, and a margin should be allowed for delay.

Arrangements must be made with the shipping authorities for the adequate storage of this on the ship, and it is necessary to take care that only sound food is given and that it is stored in a dry place on board; this applies to bedding as well as food.

Full written instructions for feeding, watering, and cleaning should be fixed to the *front* of each box, and a copy of such instructions supplied to the Ship's Officer and the man in charge of the animals. Full power should be given to the man in charge to replenish stock of food if necessary at ports of call. When there is a question as to the amount of food required for the voyage, a Veterinary Surgeon or other competent person may be consulted.

No butcher or other member of the crew of a ship ought to be expected to take charge of more than ten head of large animals. In the case of larger consignments arrangements must be made for adequate assistance.

Suitable Food for Ruminants consists of lucerne or clover-hay, meadow-hay, bran, chaff, crushed oats, maize, or other grain.

In the Case of Carnivorous Animals it is an advantage when possible to make arrangements with the shipping company to supply meat from the ship's store, otherwise a sufficient quantity must be taken on board and kept in the refrigerator. The same applies to fruit and eggs. Milk should be taken in the form of condensed milk.

Feeding.—Carnivora need only be fed once a day, preferably in the late afternoon.

Ruminants and all other animals are best fed three times a day—in the early morning, at noon, and in the evening.

Watering (see also under "General," p. 634).—Animals should, as a general rule, be watered three times a day, but more frequently in hot weather. Water should not be left in the cages after the animals have drunk. In the case of Carnivora, Monkeys and Rodents, shallow metal receptacles should be provided, and for Ruminants, metal-lined troughs as already described.

All drinking-vessels must be kept carefully scoured and only fresh, clean water used.

Bedding.—It is advisable to supply straw or grass as bedding for Ruminants, which should be removed every morning.

For Kangaroos oat-chaff is most suitable.

Soft hay should be used for all animals provided with sleeping-boxes.

NOTE.—Where hay or straw is used on the vessel care should be taken that none of this is removed from the ship on arrival.

Hygiene.—It is necessary to clean out all boxes or cages at least once every day. On no account must they be washed out with sea-water, and care should be taken that neither the animals nor the insides of their boxes get wet while the decks are being washed, as salt water is injurious to many animals. Disinfectants, if used at all, must be used very sparingly and with great care.

All the smaller Cats should be provided with shallow trays containing ashes, earth, or sawdust, which must be changed daily.

Protection from the Weather.—In hot weather a tarpaulin or awning stretched above the boxes, leaving an air space, adds much to the comfort of the animals.

In wet, stormy, or cold weather the canvas flaps should be let down in front and the boxes protected by canvas or tarpaulins as far as possible.

Teasing of the Animals.—Precautions should be taken to prevent passengers and crew from annoying or giving unsuitable food to the animals.

TREATMENT ON ARRIVAL AND TEMPORARY DETENTION.

It is essential that on the arrival of the ship in port animals should be removed and taken to their temporary destination with the least possible delay.

Careful handling of the crates and boxes cannot be too strongly insisted upon.

On arrival after their journey from the docks all animals should be carefully examined for traces of disease and parasites both external and internal, and veterinary advice should be taken as to the treatment of suspicious cases. They should be transferred as gently as circumstances permit from their travelling-boxes into loose-boxes or large cages, where they can rest after their voyage before being despatched to their destination. On no consideration should this delicate work of transference be left to inexperienced hands.

As regards ruminants, canine animals, and swine, this examination and enforced rest are adequately provided for in Great Britain under the Orders of the Ministry of Agriculture and Fisheries. As to animals which are not liable to such inspection, importers and customers should arrange for expert inspection before taking delivery.

Dealers in wild animals should supply instructions to purchasers as to the proper treatment of animals after purchase.

Great stress should be laid on the care of animals during their detention at the premises of the importers, and all engaged in the traffic of mammals and birds should

(*a*) employ in their establishments only persons who have a distinct aptitude for this particular work,
(*b*) allow only experienced persons to handle or transfer animals from one box or cage to another.

BIRDS.

General Recommendations.

Much suffering and mortality are caused to birds in transit to Europe through

(1) Transhipment,
(2) Overcrowding.

(1) In the hints on Mammals attention has been drawn to the evils of transhipment, and this applies to an even greater extent to birds, as many more birds than mammals reach Europe only with transhipment.

The greatest sufferers through transhipment are (*a*) Parrots from South American ports which are carried by foreign lines to Havre and transhipped under unsuitable conditions, and (*b*) Weavers and Waxbills which are taken from Dakar (and other African ports) to Marseilles, whence they are sent by train and Channel steamer to England.

We would suggest that as regards the Dakar trade arrangements might be made with steamers engaged in the ground-nut trade to bring consignments direct to home ports, or that colliers which regularly take coal to Dakar from Cardiff and now return in ballast might carry these birds at a remunerative rate. Dealers in this country might be prepared to meet shipowners over this matter.

Similar arrangements might be made from other ports.

(2) *As regards overcrowding* many instances have been brought to our notice of disgraceful overcrowding and consequent injury

to birds. This particularly applies to the "Marseilles trade." Weavers, Waxbills and small Parrots, Love-birds, etc., receive very harsh treatment at the present time.

The exact limit to numbers of any given species to be placed in a cage of given dimensions cannot be stated, as it differs according to size and other considerations. As a rough rule, in the case of small Weavers and Waxbills and Love-birds, there should be twice as much perching space as there are birds in each cage. In no case should birds have to settle on the backs of others from lack of room.

It is important to give *written* instructions to anyone placed in charge of consignments of birds, and in addition a label bearing such instructions should be fastened securely to the front of each cage.

When large consignments are shipped it is essential that a man or woman should travel with the birds and give his or her entire attention to their care. A European or an Indian should, where practicable, be engaged, whose wishes may be treated with respect by those in authority on board ship.

Birds should be accustomed to captivity and thoroughly used to their new food before being shipped.

We are advised by Dr. Hopkinson, C.M.G., D.S.O., Travelling Commissioner in Gambia, that much evil would be removed if the importation of West African birds were prohibited during the period commencing September 1st and ending March 1st. This would prevent the birds being landed in the cold season, and discourage their being captured during the breeding season.

HEALTH AND CONDITION BEFORE SHIPMENT.

Birds in poor health or those suffering from any disease should not be shipped. Apart from the cruelty entailed to the sufferer there is danger of infecting the whole consignment.

Parrots in particular are liable to contagious diseases.

Most seed-eating and soft-billed birds can be shipped immediately on arrival at a port of embarkation, but Penguins must be kept before shipment until they will feed readily from the hand.

TYPES OF CAGES RECOMMENDED.

General. See Notes on "Shape" and "Construction" of Boxes (p. 635). In the case of small birds, especially soft-billed, cleanliness is much more easily secured if a small mesh galvanised wire netting is fixed about 2 inches from the bottom of the cage. This allows the droppings to fall through and prevents the bird's feet and plumage being soiled. The floors under the netting can be easily scraped and washed clean.

All Game-birds should travel in boxes with padded tops, as described hereafter, the food and water vessels being narrow receptacles made to slide in along the front of the box. Game-birds are liable to damage themselves in large crates, and these should never be employed.

Partridges, Francolins, and the smaller Pheasants travel well in boxes 2 feet by 2 feet and 12 inches high, well padded at the top, as these birds are liable to jump up and injure their heads. For this purpose a piece of canvas stretched tightly across, making a false roof about 2 inches below the solid roof, is recommended. Otherwise this space may be filled with any soft material, such as hay, grass (see, however, p. 638), cotton, capoc, or such-like substance.

Provision must be made for cleaning, feeding, and watering.

A tray of suitable grit must be supplied.

The larger Pheasants, such as Monauls and Tragopans, are best shipped in separate compartments, each compartment being about 15 inches by 17 inches by 23 inches. A canvas flap to let down over the front of each case should be provided.

Herons, Egrets, Ibises, Cranes, and similar birds travel best in boxes with each compartment some 2 feet square and 3 feet high for the smaller kinds, and proportionately larger for the larger species. There should be a space of 6 *inches to spare above their normal height.* Such boxes can be made of thin wood, padded inside the top. The front is close-boarded half-way up, with wooden spars above.

Food and water receptacles some 8 inches deep must be provided.

There must be a space at the bottom for cleaning.

A canvas flap should not be omitted.

Penguins require to be hand-fed throughout the voyage. They should be kept a month in captivity before shipment. On board they travel best in large shallow boxes, the lids of which can be opened, or in a space boarded off on the deck. They are liable to a highly contagious mould disease, and no bird in the least "moping" should be shipped.

Waterfowl, Waders, Rails, etc., travel best in boxes about 3 feet by 2 feet by 15 inches high (accommodating eight to ten birds), the front to be of wooden bars, with a space of some 2 inches for cleaning. Long troughs should be provided for grain and other food, which is given in fresh water and given morning and evening.

Clean straw or grass should be provided for bedding.

The box should be washed out with fresh water each morning, and clean straw supplied in the evening.

Geese require a similarly constructed box but larger in size, to accommodate not more than ten birds.

Birds of Prey travel well in boxes made from packing cases, with one side partly boarded and the rest filled in with wire-netting or wooden bars. A suitable perch must be securely fixed at a height which will allow a space of some 4 to 6 inches above the bird's head, and sufficient space below for its tail. An opening must be provided for cleaning, and a door for feeding and watering.

Sawdust should be lightly sprinkled over the floor after cleaning each day.

Finches and Weavers.—Small foreign Finches such as Weavers and Waxbills are frequently transported in what are known as "Marseilles" cages, made of thin wood, about 24 inches by 15 inches by 8 inches, with sloping wire front. As a rule they travel well in these, if not overcrowded, but cages should be provided with water and seed troughs running along the front and not from front to back.

A useful type of cage can be made from what are known as "Kerosine" boxes. These are 21 inches by 14½ inches by 11 inches. One side is boarded only half-way up, the upper part being covered with wire-netting. A door is cut in the lower part of the front close to the floor, and serves for both feeding and cleaning. Three or four perches are fixed from front to back, on the same level but suitably spaced, at about 1½ inches from the floor, and only in part of the box, a space at the other end being left for feeding. A light canvas flap is provided for letting down over the front. Such cages can be made by any handy man and the boxes are obtainable almost anywhere. They can be successfully used for many types of birds, both seed-eaters and soft-bills.

We do not recommend the very large cages now in use by the trade between Dakar and Marseilles, and suggest those described above in their place.

Soft-billed Birds, Thrushes, Indian Shamas, etc. are imported in cages with numerous separate compartments, the number of which is immaterial, each compartment measuring 12 inches by 7 inches by 7 inches, and containing one bird only. These are made of thin wood, the fronts only being wired. Food and water vessels fit into the front, and there is a space left for cleaning. Such cages appear to be quite satisfactory.

Pigeons.—Low box cages with padded tops; perches some 3 or 4 inches from the bottom, suitable food and water receptacles, and a space for cleaning.

Grit being necessary for these birds, a suitable receptacle should be provided.

Hornbills and Toucans are best transported singly in box cages with suitable perches, rather deep receptacles for food and water, and provision for cleaning. Wooden bars in front are advisable. A large Hornbill requires a strong box cage 3 feet high by 2 feet square.

Jays, Magpies, Starlings are best imported singly or in pairs in box cages with wired fronts and suitable perches. A suitable size for a pair of Jays would be 2 feet 6 inches by 1 foot 6 inches.

Brazilian Parrots and Australian Gallahs are commercially imported in box cages about 3 feet 6 inches by 2 feet 6 inches by 18 inches, some twenty birds being placed in each box. Not more than *ten* birds at the most should be caged together.

It would appear to be inadvisable to cage these birds in pairs, as when this is done the stronger individual is apt to prevent the weaker from feeding, and may subject it to constant "bullying." They travel well in single compartments of the box type about 12 inches square.

A box cage 2 feet 6 inches square by 18 inches high with suitable perches, a wired front, and due provision for feeding, watering, and cleaning, is suitable for ten individuals.

Sulphur-crested Cockatoos are frequently imported under most unsuitable conditions, packed in large crates without perches. As they are hardy birds they receive little care and are often injured through overcrowding. No more than ten birds should be confined in the same compartment, but they are best placed singly.

Perches of hard wood should always be provided and firmly fixed in the box.

A box 3 feet square by 2 feet high would accommodate ten birds.

Macaws are best imported in pairs in very strong cages 18 inches by 18 inches by 2 feet high, with a tough hard-wood perch.

Small Parrots and Love-Birds.—A box cage 2 feet by 15 inches by 15 inches is suitable for 15 Parrots of the size of *Pionus* or *Pæocephalus*, or twenty-five Love-birds (*Agapornis*), Ring-necks (*Palæornis*), or Rosellas (*Platycercus*).

The Short tailed Lories are best sent in pairs in box cages 12 inches by 12 inches by 12 inches, with two perches one behind and above the other.

Ostriches, Emus, Rheas, and Cassowaries require large and strong boxes proportionate to their size. They should be close-boarded, except for the top half of the front, which should have wooden bars. There should be openings in the front about half-way up, in which movable food and water-vessels can be fixed on the inside, and a small door formed near the floor for cleaning.

FEEDING.

Due provision for cleaning, feeding, and watering must be made. The common practice of covering the entire floor of the cages with seed, which is not replenished at least daily, is injurious and wasteful. Seed should be placed in a tray at one end of the cage only, above which no perches should be placed.

Fresh seed should be given at least three times a day and clean water twice a day, and more often in hot weather, the receptacles having been first emptied and cleaned. Water should always be available; the practice of placing water-troughs in the cages for a short period and taking them out again is a bad one.

A supply of food sufficient to last the journey and allow of delay due to bad weather or transhipment must be taken on board. The following is suitable for the various kinds mentioned below:—

FOOD.

Game-birds.—Grain such as wheat or dari. Green food when possible, sweet potatoes, fruit. Coarse sharp grit is essential.

Cranes.—Grain such as wheat, dari, maize, and a meal made of barley-meal and ground meat.

Penguins.—Suitable fresh fish the size of herrings.

Waders.—Finely-chopped hard-boiled egg, meat, and biscuit-meal.

Ducks and Geese.—Grain such as wheat, barley, and buck-wheat, given in a shallow tray with water. Sharp grit given in water is desirable.

Finches and Weavers.—Millet (white and Indian) and canary-seed.

Soft-billed Birds.—Indian birds are usually imported on "Sattoo," an Indian mixture. In Europe they are fed on a food consisting of biscuit-meal, preserved yolk of egg, preserved ants' eggs, mixed with beef suet. On board ship hard-boiled egg, ground meat, and powdered biscuits.

Pigeons.—The larger species require wheat and dari; the smaller thrive on canary and millet seed. They should always have access to clean sharp grit.

Herons, Ibises, Egrets.—Chopped meat and fish.

Hornbills and Toucans.—Fruit, especially bananas, grapes, cut-up apple, and hard-boiled egg. Hornbills also require a small quantity of meat.

Jays, Magpies, Starlings.—Minced meat, hard-boiled eggs, fruit, and biscuit-meal.

Parrots.—Sunflower-seed, canary-seed, hemp, boiled maize, nuts, fruit. Young birds will, as a rule, only take soft food such as boiled maize and soaked biscuits. If fed on dry food they require a regular supply of water.

Lories and Lorikeets require a sop made of broken biscuit and boiled (condensed) milk, and fruit.

WATERING.

All birds should be supplied with fresh clean water twice a day, or more often in very hot weather. When possible they should be given occasionally, especially in sunlight, a shallow receptacle for bathing.

STORAGE ON BOARD SHIP.

Cages should be stacked with proper protection against both heat and cold. The habit of covering cages closely with tarpaulins in hot weather causes undue suffering to the occupants. It should be found possible to rig up an awning on deck to serve both purposes—shelter from sun, rain, and wind. Cages should not be stacked on hatches—a bad system which occasions the birds being hurriedly moved when the vessel is in port discharging or taking on cargo, with consequent exposure. It is not advisable to store the birds near the donkey-engines as the noise of these working causes panic to shy birds. In cold weather space should be found below, where air and light are forthcoming.

ATTENTION AFTER ARRIVAL.

It is important that on the arrival of the ship birds should be met by the consignee and quickly removed to their destination.

The largest importers in Great Britain—and there are very few—make good arrangements for the temporary detention of birds on their premises, but we are doubtful of the conditions existing in the smaller shops which get their supply direct from the large importers. In some of these the birds are housed in very cramped quarters and under miserable conditions. The cages are not properly cleaned and are kept in dark airless premises. Such conditions are even worse on the continent.

We strongly recommend that on arrival birds should be placed in clean roomy cages, which should be larger than those in which they had travelled; that they should have plenty of fresh air and light, and warmth in the winter time. Due attention must be paid to regular cleaning, feeding, and watering, as we have recommended for birds during transit, in addition to which they should be given shallow trays for bathing.

Sun-birds, Birds of Paradise, and Humming-birds, require the care of an experienced attendant.

REPTILES.

GENERAL.

In every case a tin for water should be fixed by wooden struts in one corner, beneath a wire-gauze covered hole, through which it may be filled with water. Water is very necessary. It is not advisable in many cases to water the whole box indiscriminately.

Travelling-boxes should be made of wood free from "knots," as these frequently get knocked out *en route*, and escapes have been known on this account. It is also advisable in making air-holes, or leaving slits, to take babies that may be born on the voyage into consideration. We know of several cases where great trouble has been caused on a ship by the birth, and escape, of baby Rattlesnakes and Russell's Vipers.

Padding of boxes and tins is also necessary in many cases detailed below. Also perches to prevent undue shaking.

If possible tins should be avoided and wooden boxes used. Tin is a good conductor of heat, and the temperature in receptacles made of that metal is subject to more sudden changes than in wooden boxes.

Boxes containing reptiles should never be left standing in the sun. They should always be kept under cover.

Artificial warmth is necessary in the colder latitudes.

PARASITES.

Snakes, lizards, and tortoises often are infested with ticks which may multiply so as to affect their health. It is possible to pick these off by hand, but the wounds left often become septic. The best methods are to apply paraffin to each tick, which can be conveniently done with a swab of cotton wool, or to crush each tick with a forceps. Either method kills the ticks, which soon drop off without leaving damaged spots.

CROCODILES AND TORTOISES.

These can be crated up and watered daily with a hose. No special drinking tin is required. Large Crocodiles should be crated each one separately. With young ones and with small Tortoises and Terrapins there should be no overcrowding, and a door should be provided for the removal of dead specimens.

On short voyages no food is required. On long ones Crocodiles and Terrapins may be fed on meat, and Land Tortoises upon vegetables and some fruits, such as bananas, or even bread and jam. Weather and other circumstances permitting Land Tortoises should from time to time be taken from their boxes and allowed to exercise on deck. Under such conditions the Tortoises will become tame enough to feed from the hand.

LIZARDS.

Water tins are very important.

Very large Monitor Lizards should each be boxed separately. Where several smaller Lizards are packed together, dry leaves, moss, and some fixed perches make a great difference in the amount of shaking about they will receive, as it gives them something to hold on to. An elaborate system of thin brushwood perches is an absolute necessity for *Chameleons*, *Anoles*, and South American *Iguanas*.

Geckos of all kinds travel best in boxes made on the shelf, or bunk, system with a water tin on the floor.

Chameleons and *Anoles* require sprinkling with water once a day as they will not drink out of a dish.

Forcible feeding is not advisable.

Feeding on short voyages is unnecessary.

Monitors eat meat or raw eggs.

Iguanas and Mastigures eat lettuce and other vegetables.

Small Lizards, Chameleons, and Geckos as a rule eat insects, and will generally take ship's cockroaches of suitable size.

All Lizards (excepting the *Heloderm*) are non-poisonous and can be handled and kept clean if required. (Very large Lizards give bad bites and scratches, but small ones are harmless.)

Regarding boxes. Wire, etc., should be avoided inside the cage of excitable Lizards likely to hurt their noses in trying to get out. Mosquito netting stretched tight inside the cage in front of the wire will prevent such injuries.

It is important to keep all boxes warm as soon as colder latitudes are reached.

SNAKES.

Most of the rules laid down for Lizards also apply to Snakes.

Water is important, and good, well-made boxes. Also fixed brushwood perches in the case of all small, fragile, or arboreal specimens.

As some Snakes are poisonous, none should be unpacked or handled on the voyage, and water should be poured into the water tins through a wire-gauze window. It is best not to pack many together on account of deaths.

When poisonous Snakes are sent the box should be covered outside with wire gauze, and where there is a wire-gauze top this should be double, and the two layers at least one inch apart to prevent risks of bites. Spitting Cobras should be further covered (over any wiring) with sacking. All should be labelled as to contents.

Large Pythons and Anacondas and Corais Snakes of America have easily damaged noses and soft skins. In their case no wire should be used. Simple cracks and slits should be left for air, and the boxes should be well padded inside with hay (but see p. 638) and sacking or felt. This might well apply to any Snake which looks smooth and shiny rather than rough.

In the case of short journeys—ten days or less—snakes will travel in comfort in large bags, each snake in a separate bag, made of some material that allows for the free passage of air, the bags being placed inside wooden boxes.

It is unnecessary and inadvisable to feed Snakes on a voyage. Long fasts do not injure them.

BATRACHIANS.

FROGS, TOADS, NEWTS, AND SALAMANDERS.

The whole of these are harmless and insectivorous. They do not drink. There is one essential factor in sending them for any distance alive. They must *always be kept damp* or they are unable to breathe through their skins, and soon dry up and die.

To maintain a moist atmosphere damp white blotting-paper crushed into balls, or damp sponges are useful. It is convenient to tie the sponge to a piece of string attached to a perforated aperture in the roof of the box. The sponges can thus be easily got at for moistening. Moss, except for short journeys, is apt to go foul and cannot be relied upon.

Very large Frogs (Bull-frogs, etc.) require special treatment. They jump and wear away their noses on the lids of travelling-cans, etc. They should be packed in wooden tubs with sacking covers, and 2 inches of fresh water at the bottom, changed when foul. Dead frogs should be removed (and if rare put in ice).

If air-holes are bored in a tin they should always be pierced *from* inside, out, so that there are no sharp edges.

Forcible feeding is dangerous, and food is unnecessary. But small cockroaches and flies can be given.

FISH.

Carriers.—A plentiful water surface is essential for the well-being of all fish, which should be transported in vessels which are broad rather than deep. Thus a milk-churn is not a suitable carrier. In the case of marine fish a discreet choice of the metals used in the manufacture of the travelling-tanks must be made, for if copper or zinc come into contact with the sea-water the inhabitants are speedily poisoned. The most suitable tanks for transporting marine specimens are those manufactured of seasoned wood or of iron lined with enamel or fired with bitumastic. A good type of carrier is one in which a grid of perforated metal is fixed, about 3 inches from the bottom, forming a false bottom. The excretory products will sink, and this false bottom will prevent the fish from lying in or disturbing the harmful products.

Water.—The water in the travelling containers must be clear and pure. Old water should, if possible, be used, and therefore it is best not to change the water unless there is danger of it becoming foul. Distilled water and salt water condensed, as often obtainable on board ship, are injurious to fish.

Preparing Fish for a Journey.—Fish should be prepared for a journey by being starved for four or five days. This gets them into travelling condition and prevents them from fouling the water in the containers in transit.

Numbers. — The wages of overcrowding, especially on long journeys, are death. It is a sound rule to allow one gallon of water for every inch of fish. (To find the gallon capacity, multiply the length, breadth, and height of the container together in inches, and divide the result by 231). If "regrettable incidents" are to be avoided on no account must harmless fish such as carp or tench be placed in the same tank with such aggressive carnivorous feeders as perch or pike.

Temperatures.—Apart from overcrowding sudden changes in temperature are the chief causes of misfortune on the voyage. To submit fish to sudden changes in temperature either by changing the position of the tanks from a hot locality to a cool one or *vice versâ*, or by adding large quantities of warmer or colder water, is almost certain to encourage fungus (*Saprolegnia*), congestion of the gills, and other usually fatal diseases. Care should be taken to ensure that the travelling-tank is not placed in a position where it receives direct sunshine.

The consignment of temperate fish in warm weather should be avoided if possible. If necessary to do so the temperature may be reduced by allowing the water from melting ice to drip through the perforations in the lid of the carrier. A lump of ice as large as a coco-nut and wrapped in a towel to prevent too-rapid melting will keep 20 gallons of water cool in very hot weather for five or six hours.

Tropical fish must usually be kept at a comparatively high temperature—70°-80°. Such temperatures may be maintained on short journeys by wrapping hot-water bottles round the carriers, or by adding at intervals small quantities of very hot water from a thermos flask. On board ship there should be no difficulty, as the temperature may be maintained by keeping the containers in the neighbourhood of heated pipes.

Aeration.—In the case of goldfish, carp, tench, and other fish inhabiting still water no special steps need be taken to aerate or change the water in the containers provided the journey is one of less than 12 hours, and that the temperature is below 65° F. In the case of long journeys, fish, especially marine forms and those inhabiting running water, should be accompanied and the water aerated with a pump at frequent intervals. A small electric pump driving a small compressor and receiving its current from a lighting-point is excellent for use on board ship. Care should be taken to ensure that the voltage and current of the motor agree with those of the lighting on board the ship. Trout and other fish requiring very much aeration may be successfully consigned long distances in closed cans with oxygen chambers. The can is first filled with water and the oxygen is passed into the chamber by means of a flexible tube connected to the oxygen cylinder. The oxygen forces out the water from the chamber and replaces it.

Food.—Fish are capable of fasting for very long periods and should not be fed on journeys of less than a fortnight's duration. On longer voyages they may be offered very finely minced liver and heart. Members of the carp family will enjoy unsweetened biscuit and lettuce. Discarded fragments of food and other foul matter must not be allowed to remain in the tank. They may be removed by means of a rubber syphon-pipe, one end of which should be run over the bottom so that it sucks up all waste matter in the manner of the household vacuum-cleaner.

EXHIBITIONS AND NOTICES.

March 20th, 1928.

Major S. S. **Flower**, O.B.E., Vice-President,
in the Chair.

The **Secretary** read the following Report on the Additions to the Society's Menagerie during the month of February, 1928:—

The registered additions to the Society's Menagerie during the month of February were 58 in number. Of these 28 were acquired by presentation, 18 were purchased, 6 were deposited, 2 were received in exchange, and 4 were born in the Menagerie.

The following may be specially mentioned:—

2 Giraffes (*Giraffa camelopardalis*), ♂ ♀, from Southern Rhodesia, deposited on February 20th.

The **Secretary** exhibited, and made remarks upon, a series of Photographs of the Detroit Zoological Gardens.

April 3rd, 1928.

Prof. E. W. **MacBride**, F.R.S., Vice-President,
in the Chair.

Miss E. M. **Brown** (Aquarium Research Fellow) exhibited, and made remarks upon, a Fluke (*Microcotyle* sp.) from the Gills of the Sea Bream (*Pagellus centrodontus*).

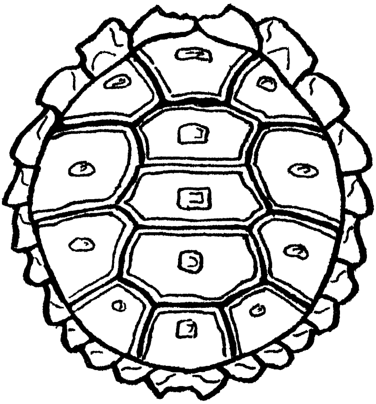
Mr. F. **Martin Duncan**, F.Z.S., exhibited, and made remarks upon, specimens of Trapdoor-Spiders' nests from Queensland, and a female Huntsman Spider (*Heteropoda venatorius*) with her egg-cocoon.

Mr. D. **Seth-Smith**, F.Z.S., exhibited, and made remarks upon, (1) a lead-pipe gnawed by mice, and (2) photographs of the Society's New Bird House.

Mr. E. G. **Boulenger**, F.Z.S., exhibited, and made remarks upon, living specimens of the Toad, *Pipa americana*.

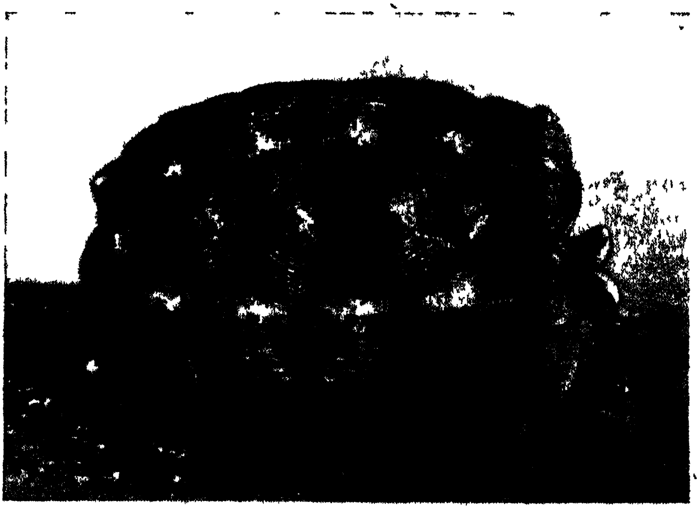
Major S. S. Flower, O.B.E., F.Z.S., exhibited a living specimen of the Great African Tortoise (*Testudo sulcata*) to show:—(1) rate of growth, and (2) the tooth-like processes of the horny jaw. Major Flower stated that newly-hatched individuals have a carapace about 50 mm. in length by about 47 mm. in extreme width. The individual exhibited (text-fig. 2), a male, was hatched in the Giza Zoological Gardens, Egypt, on October 5th, 1910; on March 26th, 1928, it weighed 184 lbs., and measured 30 inches in length.

Text-figure 1.



Testudo sulcata. Carapace, natural size, of tortoise on the day it hatched from the egg.

Text-figure 2.



Mr. D. SETH-SMITH, F.Z.S., communicated the following "Note on Nkosi Island and its Sitatunga (*Tragelaphus spekii*)," by Captain C. R. S. PITMAN, D.S.O., M.C., C.M.Z.S.:—

NOTE ON NKOSI ISLAND AND ITS SITATUNGA (*Tragelaphus spekii*).

It was only possible to make a brief visit lasting four hours on the 9th of April, 1927, but, owing to the fact that the island is not much more than 1½ miles in length and only a few hundred yards in breadth, while there is little restriction of movement owing to the depredations of the buck, it was not difficult to make a fairly comprehensive survey of the sitatunga,

As one approaches Nkosi from the lake there is nothing to suggest that it should differ from the typical forest-clad islets of the group—and dense green foliage apparently extends right down to and overhangs the water's edge.

The only convenient landing place is on the N.W. side of the southern extremity, and it must be borne in mind that it is only possible to visit the island in fair weather.

One had scarcely entered the cover of the island before one realised that though the sitatunga can be held responsible for a general absence of foliage from the ground-level to as high as they can reach when standing on their hind legs, there is another factor which creates havoc amongst the trees, especially the larger ones, and that is water-spouts and hurricane-like gales, which, judging from appearances, are evidently of frequent occurrence. Of the huge forest giants there are but few left standing—the majority, and especially at the southern end, are lying flat; not only that, the appearence of the tops of the taller and larger trees would almost lead one to believe that they had been subjected to severe shell fire, and on the ground beneath lies a tangle of branches and shattered limbs.

I was accompanied by an Officer of the K. A. Rifles, the possessor of a useful pocket cinematograph camera; six natives were also landed to act as beaters.

The island towards the centre narrows to less than one hundred and fifty yards in width—an excellent place from which to observe driven animals, as there is a high central ridge with a sharp drop and bare ground to the lake edge on one side, and a thicket-covered slope on the other. The buck when disturbed move along between the ridge and the thicket or through the thicket.

As the lack of time precluded the possibility of searching for other landing-places on the island, and as it was soon realised that the majority of the buck were concentrated at the northern end where the cover was extremely dense, the "modus operandi" was to leave the camera expert at the neck and move northerly along the S.E. edge of the island with the beaters, disturbing as few sitatunga as possible, and, finally, to extend a line of men (only seven of us all told) from shore to shore and quietly drive the buck towards the watcher.

This plan would have worked admirably but for the fact that, in typical native fashion, three of the beaters lagged behind and became hopelessly lost, and these were responsible for generally disturbing the sitatunga and causing some dozens to break back in the course of the beat.

It was estimated that there must be fully one hundred and fifty sitatunga on the island. More than forty passed the camera; at least thirty went ahead of our party into the dense cover of the northern end and were not included in the drive; just under fifty animals were observed to break back; and it can be accepted that many of the island's inhabitants were not seen, and thirty is not likely to be an overestimate of that number.

Sitatunga were observed slinking away from us in the cover within a few minutes of setting foot on the island. It was noticeable that the animals preferred to move by easy paths or broad lanes through the cover and avoided the tracks which lead through a tangle of creepers and dense bush.

One of the first males put up was startled out of a thicket and crashed away uttering a muffled bark not unlike the grunt of a pig. This bark was heard on two other occasions, once a sharp, staccato sound evidently emanating from a female.

The colour of the males is greyish—almost the grey of a donkey; many heads were observed over 24 inches in length, and at least three must have taped fully 28 inches. The marked preponderance of males struck both my companion and myself, and may be explained by the fact that it was evidently the season at which the young are dropped, and possibly the expectant females were concealed in the dense thickets at the northern end. Of the forty odd animals which passed the camera the majority were bucks, and experience in the beat tended to show that it was members of this sex which were continually breaking back.

Particular notice was taken of the general appearance of the sitatunga, and though in a few individuals the build was slighter than in others, one cannot claim that the creatures appeared ill-nurtured or exhibited any marked thinness. At present this race appears healthy enough and capable of reproduction, as testified by the presence of numerous juveniles, some only just dropped and the size of tiny kids.

Major Meinertzhagen has referred to the extreme tameness of the sitatunga on Nkosi. From my own experience these antelopes are to-day in no whit more shy, and time and again individuals stood and looked at me from a distance of a few feet. In several instances hand-clapping and shouting produced no effect, and I saw one of the beaters hit one buck several times with a stick before he could turn it and drive it in front of him. This exhibition of boldness was almost wholly confined to the males, and the females were noticeably shyer.

The tiny juveniles were delightful little creatures, bright rufous in colour and apparently spotted white. Adult females are also rufous, but on them I failed to detect any markings.

The above gives the situation on Nkosi as I found it in April, 1927.

In this connection arise two points of great importance.

One is normal increase and the other is wastage.

Of the approximate total of 120 animals seen some seventy were males, thirty-five females, and fifteen juveniles.

If one reckons the annual increase at forty (probably far below the actual figure), it would appear that within a few years, Nkosi, which is about 200 acres in extent, would resemble a cattle-pen.

This brings me to the question of wastage, and the only theory that I can propound in the matter is that crocodiles probably take a steady toll of the four-footed inhabitants of the island, while casualties in tropical storms may be more numerous than one would imagine and crocodiles would speadily dispose of the remains. I also noticed portions of the sloughed skin of a python which would indicate another source of mortality.

It might not be out of place to make a few observations on the general aspect.

These sitatunga presumably reached Nkosi by water, though it is curious that the species is not found on the neighbouring islets of Buguye, Kirugu, and Kuye, and one must go to Fumve and Ngabu, fifteen miles distant, to find its nearest habitat.

Nkosi, being the southernmost of the Sese group, is exposed to the full fury of the open lake and its frequent tropical storms.

There is no papyrus, no swamps, no secluded reedy bays—only a rocky foreshore and rough water—a more unsuitable habitat for the sitatunga one could hardly conceive.

If these antelopes were desirous of taking to the water, they would be forced out at once by its roughness and by the presence of crocodiles, and I consider that these are just as important factors in deciding their mode of life which previously has been suggested as attributable to the absence of man.

Mr. C. F. M. Swinnerton, C.M.Z.S., exhibited, and made remarks upon, photographs showing forest undergrowth cleared by the browsing of Sitatunga.

Mr. D. Seth-Smith, F.Z.S., exhibited photographs of a Pangolin, and gave an account of a specimen that had been captured by Captain C. R. S. Pitman, and had lived for a short time in captivity.

April 17th, 1928.

Prof. J. P. Hill, F.R.S., Vice-President,
in the Chair.

The Secretary read the following Report on the Additions to the Society's Menagerie during the month of March, 1928:—

The registered additions to the Society's Menagerie during the month of March were 271 in number. Of these 118 were acquired by presentation, 126 were purchased, 23 were deposited, and 4 were received in exchange.

The following may be specially mentioned:—

1 Lechwe Antelope (*Cobus leché*), ♂, from South Africa, received in exchange on March 3rd.

6 Triton Hamsters (*Cricetulus triton*), from Shantung Province, China, new to the Collection, presented by Prof. E. Hindle, F.Z.S., on March 8th.

4 Ceylonese Jungle-fowl (*Gallus lafayettei*), presented by W. Shakspeare, Esq., on March 9th.

Collections of foreign birds, presented by Alfred Ezra, Esq., O.B.E., on March 2nd, 20th, and 23rd: and by Captain H. S. Stokes, M.C., on March 9th, 21st, and 30th.

A large Salmon (*Salmo salar*), from Tavistock, presented by the President, His Grace the Duke of Bedford, K.G., on March 18th.

Mr. Clarence Elliott, exhibited, and made remarks upon, (1) specimens of Giant Barnacles from Chile, and (2) a living specimen of a Giant Tortoise (*Testudo microphyes*) from Albemarle Island (Galapagos Islands).

NOTES ON GIGANTIC LAND TORTOISES.

Lord Rothschild, D.Sc., F.R.S., F.Z.S., exhibited photographs and skulls, and made the following communication on Gigantic Land Tortoises:—

The Giant Land Tortoises of recent times were divided into three sections by Dr. Albert Günther as follows.

1. Nuchal plate present; third cervical vertebra biconvex; gular double. Seychelles—Madagascar—Aldabra races.
2. Nuchal plate absent; fourth cervical vertebra biconvex; gular double. Galapagos races.
3. Nuchal plate absent; fourth cervical vertebra biconvex; gular single. Mascarene races.

This classification holds good to-day in spite of several attempts to upset it. Of living and extinct species of No. 1 section there are seven named forms, of which *grandidieri* Vaill., *abrupta* Grand. are fossil (or subfossil) from Madagascar; *elephantina* and *daudinii* Dum. & Bibr. from N. & S. Aldabra respectively; and *gigantea* Schweig., *gouffėi* Rothsch., and *sumeirei* Sauz. were inhabitants of three islands of the Seychelles group. Of No. 3 group 11 forms have been distinguished, one of which (*microtympanum* Boul.) is altogether doubtful (probably skull of *leptocnemis*), and *africana* Schweig=*graii* Dum. & Bibr. only doubtfully belongs to the Giant Tortoises and is also of very doubtful origin.

Of the remaining nine, *indica* Schneid. is from Réunion: *vosmæri* Schoepff, *peltastes* Dum. & Bibr., and *commersoni* Vaill. are from Rodriguez; and *inepta* Günth., *triserrata* Günth., *sauzieri* Gadow, *leptocnemis* Günth., and *gadowi* Van Denb. are from Mauritius, but *gadowi* belongs with its forked *gular* to a quite different older geological horizon. All the nine more recent Mascarene Giant Tortoises were exterminated before 1830.

Of No. 1 group *elephantina* from N. Aldabra is quite extinct in a wild state, but a few *daudinii* are still left on S. Aldabra. On the Seychelles all indigenous species are now extinct, but a large number of *elephantina*, *gigantea*, and *daudinii* are kept there in a semi-domestic condition together with numerous resultant hybrids.

The tortoise exhibited to-night is one of No. 2 group and belongs to the Central Albemarle form *Testudo microphyes* Günth. (probably from Iguana Cove), and is undoubtedly one of the largest, if not the largest, surviving example of the Galapagos Giant tortoises. It weighs 380 lbs. (2½ cwt), and the carapace measures 38 inches in length in a straight line, and 48 inches over the curve, and 28 inches in width between uprights, and 48 over the curve. It is almost exactly the same size as the largest *microphyes* from Cape Rose formerly exhibited in the Society's Gardens, whose dimensions were 38½ inches, 46 inches, 28½ inches, and 43½ inches.

Of this group 13 forms have received names and descriptions, viz., *vicina* Günth., S.W. Albemarle; *güntheri* Baur., S.E. Albemarle; *microphyes* Günth., Central W. Albemarle, and *becki* Rothsch., N. Albemarle; *wallacei* Rothsch., Jervis Island; *nigrita* Dum. & Bibr., Indefatigable Island; *darwini* Van Denb., James Island; *galapagœnsis* Baur, Charles Island; *chathamensis* Van Denb., Chatham Island; *hoodensis* Van Denb., Hood Island; *ephippium* Günth., Duncan Island; *phantastica* Van Denb., Narborough Island; and *abingdoni* Günth., Abingdon Island. Of these *galapagœnsis*, *abingdoni*, *ephippium*, *phantastica*, and *becki* are saddle-backed races (*i. e.*, have the carapace shaped like a Spanish saddle).

Of the 18 races of groups Nos. 1 and 2, 12 races have been exhibited at various times in the Society's Gardens, viz., of group No. 1 *elephantina*, *gigantea*, *daudinii*, *gouffei*, and *sumeirei*, and of group No. 2 *abingdoni*, *ephippium*, *becki*, *darwini*, *microphyes*, *güntheri*, and *vicina*.

By far the largest three examples of these were (1) the large male *darwini*, of which the carapace measures in length 48½ inches in a straight line and 56½ over the curve, and 34½ inches in width between uprights and 62 inches over curve; (2) the large male *T. vicina* 46 inches in a straight line and 59 inches over the curve, and 38 inches wide between uprights and 62 inches over curve; and (3) the large male *daudinii* in which the carapace had a straight length of 52¼ inches and 66 inches over curve; a width between uprights of 36¾ inches and 61 inches over curve; and a weight of 560 lbs. This is the largest known recent land tortoise.

Lord Rothschild exhibited also the life-sized photographs of the above-mentioned *Testudo darwini* and *T. daudinii* as being the largest known Galapagos and Aldabra tortoises respectively. He also exhibited the skull of the *T. darwini*, one of a large 45½ inch *elephantina* hybrid, and one of *T. innepta* from Mauritius, to show the flat skull with protruding fore part of the Galapagos races as opposed to the more bombiform skull, truncated in front, of the Aldabra races and the very narrow skull with protruding fore part of the Mascarene races.

P.S.—The type example of *T. becki* Rothsch. and an example of *T. vicini* Günth. in the British Museum have the 3rd cervical vertebra biconvex; but this apparently is quite accidental, and it holds good in the vast majority of cases that the 4th cervical is biconvex in the Galapagos Island races.

It has recently also come to light that the original type-specimen of *T. microphyes* is rather different from the series brought back by Commander Cookson and referred to this race by Dr. Günther; in fact, tested by Van Denburg's formula, it is a small *güntheri* Baur. Should this definitely be confirmed the Central Albemarle tortoise will require a new name or else be called *macrophyes* Garman.

[‘Proceedings,’ 1928, Part I. (pp. 1–268), was published on April 16th, 1928.]

INDEX OF ILLUSTRATIONS.

Actæcia euchroa, Fig. 10, p. 580.
Agonia chlorina, Fig. 4, p. 158.
Anthropopithecus troglodytes, Pls. I.–IV., p. 1.
Apteryx oweni, Figs. 3, 10, 11, pp. 202, 214, 215.
Arhina porcelloides, Fig. 12, p. 583.
Armadillidium vulgare, Fig. 19, p. 593.
Armadilloniscus sp., Fig. 9, p. 579.
Atelecyclus septemdentatus, Pls. II., IX., X., p. 473.
Australopithecus, Pl. IV., p. 1.

Bathynectes longipes, Pl. IV., p. 473.
Bulinus natalensis, Figs. 3, 4, p. 176.

Cancer pagurus, Pls. I., V., p. 473.
Canis lupus, carcinoma of tonsil, Pls. I.–III., p. 43.
Carcinus mænas, Pls. I., VII., p. 473.
Carineta formosa, Figs. 31, 60–66, 71–75, pp. 403, 424–432, 438–442.
Casuarius, Fig. 11, p. 215.
Chondrosteus acipenseroides, Fig. 15, p. 68.
Chonosia crassipennis, Figs. 49, 59, pp. 413, 423.
Clausilia jemjemensis, Pl. I., fig. 5, p. 163; Fig. 1, p. 169.
Corystes cassivelaunus, Pl. II., p. 473.
Cosmoptychius striatus, Figs. 1–4, pp. 50–52.
Cubaris officinalis, Fig. 18, p. 591.

Deto bucculenta, Fig. 8, p. 577.
Dinocampus (*Perilitus*) *rutilus*, Pls. I.–IV., p. 597.
Dinornis, Fig. 4, p. 202.
Dromæus, Figs. 5, 19, pp. 203, 229.

Ebalia cranchii, Pls. III., XIII., p. 473.
—— *tuberculosa*, Pls. III., XIII., XIV., p. 473.
Elonichthys caudalis, Figs. 8, 9, p. 57.
Emberiza citrinella, Fig. 9, p. 209.
Ergasiloides macrodactylus, Fig. 4, p. 324.
Eurynome aspera, Pls. II., XIV., p. 473.
Eurynotus crenatus, Fig. 12, p. 62.

Fidicina semilata, Fig. 5, p. 374.

Gonoplax rhomboides, Pls. II., XI. XII., p. 473.

Homorus omeri, Pl. I., p. 163.
Hyas coarctatus, Pls. II., XIV., p. 473.

Inachus dorsettensis, Pls. III., XV., p. 473.

— *dorynchus*, Pls. III., XIV., XV., p. 473.

— *leptocheirus*, Pls. III., XIV., XV., p. 473.

Lauria wouramboulchiensis, Pl. I., p. 163.

Lembeja fatiloqua, Fig. 56, p. 420.

Ligia oceanica, Fig. 1, p. 570.

Ligidium hypnorum, Fig. 3, p. 571.

Macroctopus maorum, Figs. 1, 4, 6, pp. 259, 261, 263.

Macropodia egyptia, Pls. III., XV., XVI., p. 473.

— *longirostris*, Pls. III., XVI., p. 473.

— *rostratus*, Pls. III., XV., XVI., p. 473.

Macropus fuliginosus, Avian Tuberculosis, Pls. I.–III., p. 249.

Magicicada septendecim, Figs. 19–21, 29, 68, 69, pp. 391–392, 400, 435, 436.

Maia squinado, Pls. II., XIV., p. 473.

Melampsalta cingulata, Figs. 4, 23, 33, 35, 38, pp. 372, 394, 405, 407, 410.

— *cruentata*, Fig. 41, p. 410.

— *cutora*, Fig. 47, p. 410.

— *fuliginosa*, Fig. 45, p. 410.

— *leptomera*, Figs. 1–3, 6, 22, 30, 37, 42, 67, pp. 370–372, 375, 393, 401, 409, 410, 434.

— *muta*, Figs. 7, 10–14, 17, 44, 48, 52, 54, 58, pp. 381, 384–387, 389, 410, 411, 416, 418, 422.

— *sericea*, Figs. 9, 15, 16, 18, 24, 25, 27, 28, 36, 43, 70, pp. 383, 387, 388, 390, 395, 396, 398, 399, 408, 410, 437.

— *strepitans*, Fig. 40, p. 410.

— *subalpina*, Fig. 46, p. 410.

Microcyclops gemellus, Fig. 2, p. 321.

— *tanganicæ*, Fig. 1, p. 320.

Nematoptychius greenocki, Figs. 7, 11, pp. 56, 60.

Neoglessula (?) *curta*, Pl. I., fig. 3, p. 163; Fig. 2, p. 172.

Nothura maculosa, Fig. 17, p. 222.

Octopus vulgaris, Fig. 5, p. 262.

Œdicnemus, Fig. 17, p. 222.

Orthezia urticæ, Pls. I. II., p. 269; Figs. 1–23, pp 273–296.

Oxygnathus ornatus, Fig 10, p. 59.

Paracyclops coperes, Fig. 3, p. 323.

Periscyphis rufocauda, Fig. 17, p. 589.

Philoscia muscorum, Fig. 11, p. 581.

Pilumnus hirtellus, Pls. II., X., XI., p. 473.

Pinnotheres pisum, Pls. III., XII., p. 473.

— *veterum*, Pls. III., XII., XIII., p. 473.

Piremela denticulata, Pl. I., p. 473.

Platyarthrus hoffmanseggi, Fig. 20, p. 594.

Platysomus parvulus, Fig. 13, p. 64.

Polybius henslovi, Pl. IV., p. 473.

Porcellio flavocinctus, Fig. 14, p. 585.

Porcellionides myrmecophilus, Fig. 13, p. 584.

Portunus arcuatus, Pls. I., VII. p. 473.

— *corrugatus*, Pl. I., p. 473.

— *depurator*, Pls. I., VI., p. 473.

— *holsatus*, Pls. I. VI., p. 473.

— *marmoreus*, Pls. I., VI., p. 473.

— *puber*, Pls. I., IV., V., p. 473.

— *pusillus*, Pls. I., VII., p. 473.

Pycna madagascariensis, Fig. 57, p. 421.

Rana temporaria, Figs. 1–7, pp. 308–314.

Rhea, Pl. I., p. 185; Figs. 8, 9, 13, 14 16, 19, pp. 206, 209, 217, 218, 221, 229.

Rhyscotus ortonedæ, Fig. 15, p. 586.

Schizopera consimilis, Fig. 5, p. 326.
—— *rotundipes*, Fig. 6, p. 327.
Scleropactes sp., Fig. 16, p. 587.
Scyphax ornatus, Fig. 7, p. 576.
Squamispa ballapurana, Fig. 3, p. 156.
—— *fasciata*, Figs. 1, 2, pp. 152, 154.
Struthio, Figs. 6, 7, 12, 18, 19, pp. 203, 204, 216, 227, 229.
Succinea hararensis, Pl. I., p. 163.
Syrhaptœcus alchatæ, Fig. 1 *a*, p. 340.
—— *angulatus*, Figs. 6 *a*, 8 *a*, 9 *b* & *d*, pp. 349, 351, 352.
—— *bedfordi*, Figs. 2 *b*, 9 *c*, pp. 341, 352.
—— *brevifrons*, Figs. 1 *b*, 7, pp. 340, 350.
—— *declivis*, Figs. 5 *b*, 9 *e*, pp. 347, 352.
—— *digonus*, Figs. 3 *a*, 8 *b*, 10 *c*, pp. 343, 351, 354.
—— *excisus*, Fig. 6 *b*, p. 349.
—— *falcatus*, Figs. 2 *a*, 10 *b*, pp. 341, 354.
—— *mitratus*, Figs. 4 *a*, 9 *a*, pp. 346, 352.
—— *obtusus*, Fig. 8 *c*, p. 351.
—— *pallasi*, Fig. 5 *a*, p. 347.
Syrhaptœcus tibetanus, Fig. 3 *b*, p. 343.
—— *uncinosus*, Figs. 4 *b*, 8 *d*, 10 *a*, pp. 346, 351, 354.

Teinobasis nigra, Figs. 2, 3, p. 137.
Testudo sulcata, Figs. 1, 2, p. 654.
Tetracanthagyna bakeri, Fig. 1, p. 130.
Tettigarcta crinita, Figs. 8, 50, 53, pp. 381, 414, 417.
Thia polita, Pl. I., p. 743.
Throscoryssa citri, Fig. 5, p. 161.
Tibicen chloromera, Figs. 32, 51, 55, pp. 404, 415, 419.
Titanethes albus, Fig. 5, p. 574.
Trichoniscus roseus, Fig. 4, p. 572.
Tylos latriellei, Fig. 6, p. 575.

Viguierella paludosa, Figs. 7, 8, pp. 329, 330.
Vitrina grossepunctata, Pl. I., p. 163.

Wardichthys cyclosoma, Fig. 14, p. 67.

Xantho hydrophilus, Pl. II., p. 473.
—— *incisus*, Pls. II., XI., p. 473.

INDEX.

1928.—Pages 1-660.

[New names in clarendon type. Systematic references in italics.
(Z.S.L.) indicates additions to the Society's Menagerie.]

Acanthion sp., 149.
Acanthosphinx gussfeldti, 123.
Achæus cranchii, 551.
Achatina zanzibarica ihotelleri, 126.
Actæcia euchroa, 580.
Æpyornis, 190.
Agapornis personata, 266.
Agonia chlorina, sp. n., 157.
Alipes grandidieri, 125.
Alloniscus brevis, 582.
Alseonax subadusta, 75.
Anchicubaris, 591.
Andropadus masukensis roehlii, 77.
Anthropopithecus troglodytes, 1.
Apteryx, 188.
—— *australis*, 213.
—— *bulleri*, 209.
—— *oweni*, 209.
Archæopteryx, 228.
Arctictis binturong. 146.
Arhina porcelloides, 582.
Arizelocichla nigriceps, 77.
Armadillidium vulgare, 592.
Armadilloniscus sp., 578.
Atelecyclus septemdentatus, 524.
Atlantisia rogersi, 225.
Australopithecus, 35.

Babycurus gigas, 123.
Bathynectes longipes, 515.
Bucorvus cafer, 72.
Bulinus forskali, 177.
—— *natalensis*, 175.
—— *schackoi*, 177.
—— *sericinus*, 177.
—— *truncatus*, 177.
Buphaga erythrorhyncha, 77.
Bycanistes cristatus, 72.

Calicnemis chaseni, sp. n., 136.
Callosciurus castaneoventris castaneoventris, 147.
—— *flavimanus flavimanus*, 147.
—— *leucopus*, 147.
Calmanesia methueni, 592.
Cancer pagurus, 522.
Canis lupus, 43.
Capricornis sumatrensis, 150.
Caprimulugus europæus meridionalis, 74.
Carcinus mænas, 517.
Carineta formosa, 417.
Casuarius, 197.
Cerastus boccardi, 167.

Cerastus chefneuxi, 167.
—— *sacconii*, 167.
—— *vigonii*, 167.
Cercopithecus leucampyx (Z. S. L.), 265.
Cervulus muntjac, 150.
Chondrosteus acipenseroides, 7.
Chonosia crassipennis, 393.
Chrotogale owstoni, 146.
Cinnyris loveridgei, 77.
—— *mediocris usambaricus*, 78.
—— *obscura neglecta*, 78.
Clausilia jemjemensis, sp. n., 169.
Cobus leche (Z. S. L.), 658.
Coracias neavius neavius, 74.
Corvultur abicollis, 77.
Corvus albus, 76.
Corystes cassivelaunus, 526.
Cosmoptychius striatus, 49.
Cricetulus triton (Z. S. L.). 658.
Cubaris officinalis, 591.
Cuon rutilans, 146.
Cylisticus convexus, 584.
Cynogale bennettii, 146.
Cyponterus sphinx, 143.
Cystosoma, 392.

Denchogale frenata, 145.
Dendrolagus inustus (Z. S. L.), 265.
Deto bucculenta, 578.
Diaptomus simplex, 318.
Diatryma, 223, 235.
Dicrurus ludwigi ludwigi, 76.
Dinocampus (*Perilitus*) *rutilus*, 597.
Dinornis, 199.
Dorippe, 552.
Dremomys rufigenis, 148.
Dromæus, 197.

Ebalia cranchii, 540.
—— *tuberosa*, 539.
Elonichthys caudalis, 57.
Eremopezus, 190.
Ergasilus macrodactylus, 325.
—— *megacheir*, 325.
Ethmostigmus trigonopodus, 124.
Eubelum, 591.
Eucyclops rarispinus, 319.
Eupartheria capensis, 228.
Eurynome aspera, 543.
Eurynotus crenatus, 61.

Falco naumanni naumanni, 72.
—— *tinnunculus carbo*, 71.
Felis bengalensis, 145.
—— *marmorata*, 145.
—— *pardus*, 145.
—— *tigris*, 145.
—— *viverrina*, 145.
Flacourtia, 193.
Fruticicola scioana, 166.
—— *strigelloides*, 166.
Funisciurus palliatus (Z. S. L.), 266.

Gallus lafayettei (Z. S L.), 658.
Gazella arabica, 267.
Geococcyx mexicana, 225.
Giraffa camelopardalis (Z. S. L.), 658.
Gonoplax rhomboides, 534.
Gorgon taurinus (Z. S. L.), 265.
Granularion hians, 166.
Gulella simplicima, 164.

Halcyon albiventris orientalis, 73.
Helarctos malayanus, 146.
Herpestes exilis, 145.
—— *urva*, 145.
Heteropoda venatorius, 653.
Hipposideros armiger, 143.
—— *bicolor*, 143.
Homorus omeri, sp. n., 170.
—— *ragazzii*, 170.
—— *variabilis* var. *jickelii*, 170.
Hyas araneus, 545.
—— *coarctatus*, 544.
Hylobates concolor gabriellæ, 140.
Hylopetes alboniger, 147.
—— *spadiceus*, 147.

Inachus dorsettensis, 546.
—— *dorynchus*, 547.

Inachus leptocheirus, 548.
Isometrus maculatus, 124.

Kaliella barrakporensis, 166.

Lanius collaris humeralis, 76.
Lauria bruguierei, 168.
—— **wouramboulchiensis**, sp. n., 168.
Lembeja, 392.
Leptotrichus franzerii, 594.
Lepus vassali, 149.
Ligia oceanica, 569.
Ligidium hypnorum, 571.
Lophoceros melanoleucos, 73.
Lutra sumatrana, 147.
Lybius abyssinicus (z. s. l.), 265.
Lymnæa caillaudi, 174.
—— *truncatula*, 174.

Macaca fascicularis, 142.
—— *mulatta*, 142.
Macroctopus, subg. n., 257.
Microcyclops attenuatus, 319.
—— **gemellus**, sp. n., 321.
—— **tanganicæ**, sp. n., 319.
Macromia moorei malayana, subsp. n., 133.
Macropodia egyptia, 550.
—— *longirostris*, 549.
—— *rostratus*, 550.
Macropus fuliginosus, 254.
Magicicada septendecim, 370.
Maia squinado, 542.
Melampsalta cauta, 407.
—— *cingulata*, 369.
—— *coriaria*, 422.
—— *leptomera*, 369.
—— *muta*, 382.
—— *scutellaris*, 459.
—— *sericea*, 407
—— *strepitans*, 472.
Melittophagus lafresnayii oreobates, 73.
Melogale pierrei, 146.
—— *personata laotum*, 146.
Menetes berdmorei, 148.
Merops apiaster apiaster, 74.
Mesites, 225.
Mesocyclops tenellus, 319.
Mesogereon, 395.
Mesogomphus henryi, sp. n., 131.
Microcercus anomalus, 591.
Microcotyle sp., 653.
Monochirus capensis, 159.
Mullerornis, 193.
Mus dubius, 149.

Nematoptychius greenocki, 55.
Neoglessula (?) curta, sp. n., 171.
Notogonia memnonia, 361.
—— *nigricans*, 362.
—— *nigrita*, 360.
—— *opalipennis*, 360.
—— **prætermissa**, sp. n., 361.
—— *subtessellata*, 360.
—— *trivittata*, 361.
Nyctereutes procyonoides, 146.

Octopus (*Macroctopus*) *maorum*, 258.
Oniscus asellus, 584.
Opisthocomus, 213.
Ornithosuchus, 228.
Orodesmus ornatus, 126.
Orolestes wallacei, 134.
Orthezia urticæ, 269.
Otocyon megalotis (z. s. l.), 265.
Oxygnathus ornatus, 58.

Pagellus centrodontus, 653.
Paguma larvata yunalis, 145.
Paracyclops coperes, sp. n., 322.
Paradoxurus birmanicus, 145.
Pardictis pardicolor, 145.
Periscyphis rufocauda, 588.
Phascolarctos cinereus (z. s. l.), 265.
Phatages crassicaudata, 150.
Pheidole megacephala var. *punctulata*, 121.

Phidodonta chirinda, 159.
Philoscia muscorum, 582.
Phryniscus bacillifer, 124.
Pilumnus hirtellus, 532.
Pinnotheres pisum, 536.
—— *veterum*, 537.
Pipa americana, 653.
Pipistrellus coromanchus tramatus, subsp. n., 144.
—— *tralatitius*, 143.
Pirimela denticulata, 519.
Pisa biaculeata. 544.
Pisidium pirothi, 178.
Pithecus francoisi, 142.
—— *germaini*, 142.
—— *poliocephalus*, 141.
Planorbis abyssinicus, 174.
—— *gibbonsi*, 175.
—— *herbini*, 175.
—— *rüppelli*, 175.
Platyarthrus hoffmanseggi, 594.
Platycyclops oligarthrus, 322.
Platysomus parvulus, 64.
Poëphila gouldiæ, 266.
Pogonocichla cucullata orientalis, 79.
Polybius henslowi, 516.
Porcellio flavocinctus, 584.
Porcellionides myrmecophilus, 584.
Portumnus biguttatus, 518.
Portunus arcuatus, 496, 510.
—— *corrugatus*, 496, 509.
—— *depurator*, 496, 514.
—— *holsatus*, 496, 513.
—— *marmoreus*, 496, 512.
—— *puber*, 496, 506.
—— *pusillus*, 496, 511.
Presbytes thomasi (z. s. l.). 266.
Presbytiscus avunculus, 140.
Procordulia heterodoxa, 132.
Psalidprocne holomelæna massaica, 75.
Psammornis rothschildi, 193.
Pteropus vampyrus malaccensis, 142.
Ptychotrema denticulatum, 164.
—— —— var. ex forma *nana* nov., 164.
Punctum cryophillum, 167.
Pycna madagascariensis, 398.
Pygathrix nigripes, 141.

Rana temporaria, 307.
Rattus bowersi, 149,
—— *edwardsi*, 149.
—— spp., 149.
Ratufa bicolor smithii, 147.
—— *gigantea*, 147.
Rhea, 192.
—— *fossilis*, 193.
—— *subpampeana*, 193.
Rhinolopus affinis, 143.
Rhizomys senex, 149.
Rhopalimorpha, 375.
Rhyscotus ortonedæ, 586.
Riparia fuligula fuligula, 74.
Rousettus leschenaulti, 142.
Rusa sp., 150.

Saidjahus creper, 590.
Salmo salar (z s. l.). 658.
Schizopera consimilis, 326.
—— *inopinata*, 327.
—— **rotundipes**, sp. n., 327.
Scleropactes sp., 586.
Scolopendra morsitans, 124.
Scotophilus kuhli, 144.
Scyllarus, 267.
Scyphax ornatus, 576.
Scyphoniscus waitatensis, 580.
Simia satyrus (z. s. l.), 266.
Sphærium pharaonum, 177.
—— *subcapense*, 177.
Sphæroniscus sp., 588.
Squamispa, gen. n., 151.
—— **ballapurana**, sp. n., 155.
—— **fasciata**, sp. n., 154.
Stephanoaëtus coronatus, 71.
Stringops, 224.
Struthio, 189.
—— *asiaticus*, 193.
—— *karatheodoris* 193.
Struthiolithus, 192.
—— *chersonensis*, 193.
Suarezia heterodoxa, 590.
Subulina chiarinii, 171.
—— *munzingeri*, 171.
Succinea hararensis, sp. n., 172.
Sus cristatus, 149.

Sus vittatus (Z. S. L.), 265.
Suthora webbiana (Z. S. L.), 266.
Syrrhaptœcus, gen. n., 337.
—— *alchatæ*, 344.
—— **angulatus**, sp. n., 353.
—— **bedfordi**, sp. n., 342.
—— **brevifrons**, sp. n., 339.
—— **declivis**, sp. n., 348.
—— **digonus**, sp. n., 345.
—— **excisus**, sp. n., 354.
—— **falcatus**, sp. n., 345.
—— **mitratus**, sp. n., 348.
—— **obtusus**, sp. n., 354.
—— *pallasi*, 353.
—— **tibetanus**, sp. n., 342.
—— **uncinosus**, sp. n., 350.

Tamiops inconstans, 149.
—— *maritimus*, 148.
—— *rodolphei*, 149.
Tchitrea perspicillata suahelica, 75.
Tefflus oblongicollis, 122.
Teinobasis nigra, sp. n., 136.
Testudo abingdoni, 659.
—— *abrupta*, 658.
—— *becki*, 659.
—— *chathamensis*, 659.
—— *commersoni*, 659.
—— *darwini*, 659.
—— *daudinii*, 659.
—— *elephantina*, 659.
—— *ephippium*, 659.
—— *galapagoensis*, 659.
—— *gigantea*, 659.
—— *gouffei*, 659.
—— *güntheri*, 659.
—— *hoodensis*, 659.
—— *indica*, 659.
—— *innepta*, 659.
—— *leptocnemis*, 659.
—— *microphyes*, 658, 660.
—— *nigrita*, 658.
—— *phantastica*, 659.
Testudo sulcata, 654.
—— *sumeirei*, 659.
—— *vicini*, 660.
Tetracanthagyna bakeri, sp. n., 129.
Tetrapteryx paradisea (Z. S. L.), 265.
Tettigarcta crinita, 380.
Tettigonia sp., 121.
Thia polita, 528.
Thopha saccata, 428.
Throscoryssa, gen. n., 159.
—— **citri**, sp. n., 160.
Tibicen, 392.
—— *chloromera*, 394.
Titanethes albus, 573.
Tragelaphus spekii, 655.
Tragulus kanchil pierrei, 149.
Trichoniscus roseus, 572.
Tupaia belangeri tonquinia, 144.
Turacus hartlaubi, 72.
Tylos latreillei, 574.

Veronicella sp., 173.
Viguierella paludosa, 328.
Viguierellidæ, fam. n., 331.
Vitrina bianchii, 164.
—— **grossepunctata**, sp. n., 165.
—— *modesta*, 164.
—— sp., 165.
Viverra zibetha, 145.
Viverricula malaccensis, 145.
Vulpes sp., 146.

Wallacea bowringi, 159.
Wallaceana, nom. n., 159.
Wardichthys cyclosoma, 66.

Xantho hydrophilus, 531.
—— *incisus*, 530.

Yanga pulverea, 398.

PRINTED BY TAYLOR AND FRANCIS, RED LION COURT FLEET STREET.

No. 294.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

February 7th, 1928.

Prof. J. P. HILL, F.R.S., Vice-President, in the Chair.

The SECRETARY read a Report on the Additions to the Society's Menagerie during the months of October, November, December, 1927, and January, 1928.

Mr. D. SETH-SMITH, F.Z.S., exhibited, and made remarks upon, a living specimen of a Blue Variety of the Masked Love-bird (*Agapornis personata*) and the skin of an abnormal Gouldian Grass-Finch (*Poëphila gouldiæ*) displaying hermaphrodite characters.

Major S. S. FLOWER, O.B.E., F.Z.S., exhibited three photographs taken by Mr. Geoffrey C. Flower in the Red Sea. Two were of a young Arabian Gazelle, *Gazella arabica*, from Farsān Island, the type-locality of the species; and one of a Flat Lobster, *Scyllarus* sp., which had weighed about 3½ lbs.

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Dr. P. R. LOWE, F.Z.S., gave a *résumé* of his paper "Studies and Observations bearing on the Phylogeny of the Ostrich and its Allies."

Mr. S. ZUCKERMAN, M.A., the Society's Anatomist, communicated his paper on "The Age-changes in the Chimpanzee, with special reference to Growth of Brain, Eruption of Teeth, and Estimate of Age, with a Note on the Taungs Ape."

In the absence of the Authors, the following Paper was taken as read:—F. F. LAIDLAW, M.A., F.Z.S., and H. CAMPION, "Notes on Oriental Dragonflies (Odonata) with Descriptions of New Species."

The next Meeting of the Society for Scientific Business will be held on Tuesday, February 21st, 1927, at **5.30** P.M., when the following Communications will be made:—

The Hon. IVOR MONTAGU, F.Z.S.

Exhibition of photographs of the Moscow Zoological Gardens.

G. C. ROBSON, M.A., F.Z.S.

Observations on the Oviposition of *Octopus*.

Prof. D. M. S. WATSON, F.R.S., F.Z.S.

On some Points in the Structure of Palæoniscid and allied Fish.

OLDFIELD THOMAS, F.R.S., F.Z.S.

The Delacour Exploration of French Indo-China Mammals. II. On Mammals collected during the Winter of 1926–27.

S. MAULIK, F.Z.S.

New Chrysomelid Beetles from India, with a Note on the Scales of Coleoptera.

The following Papers have been received:—

H. HAROLD SCOTT, M.D., F.R.C.P.S., F.Z.S.

Report on the Deaths occurring in the Society's Gardens during the year 1927.

H. HAROLD SCOTT, M.D., F.R.C.P., F.Z.S.

Carcinoma of the Tonsil in a Common Wolf (*Canis lupus*).

Major M. CONNOLLY.

On a Collection of Land and Freshwater Mollusca from Southern Abyssinia.

ENID K. SIKES, B.Sc.

The External Morphology and Life-history of the Coceid Bug *Orthezia urticæ* Linn.

H. C. JAMES, B.Sc., Ph.D., N.D.A., N.D.D.

On the Post-Embryonic Development of tho Female Genitalia and of other Structures in the Chalcidoid Insect *Harmolita graminicola* Gir.

DOROTHY J. JACKSON.

The Biology of *Dinocampus* (*Perilitus*) *rutilus* Ness, a Braconid Parasite of *Sitona lineata* Linn.

MARIE V. LEBOUR, D.Sc., F.Z.S.

The Larval Stages of the Plymouth Brachyura.

A Further Series of Reports on the Zoological Results of the Cambridge Expedition to the Suez Canal, 1924, by Prof. ARTURO PALOMBI, Dr. A. SCHELLENBERG, and F. A. POTTS, M.A.

H. A. HARRIS, F.Z.S.

The Closure of the Cranial Sutures in relation to the Evolution of the Cortex Cerebri and Aphasia.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
February 14*th*, 1928.

No. 295.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

February 21st, 1928.

Major S. S. Flower, O.B.E., Vice-President,
in the Chair.

Dr. G. M. Vevers and Mr. L. C. Bushby exhibited, and made remarks upon, specimens of the Mitten Crab (*Eriocheir japonicum*).

The Hon. Ivor Montagu, F.Z.S., exhibited, and made remarks upon, a series of photographs taken during a recent visit to the Moscow Zoological Gardens.

Mr. G. C. Robson, M.A., F.Z.S., exhibited a series of lantern-slides illustrating his remarks upon "Some Observations on the Oviposition of *Octopus*."

Prof. D. M. S. Watson, F.R.S., F.Z.S., communicated his paper "On some Points in the Structure of Palæoniscid and allied Fish."

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

In the absence of the Authors the following Papers were taken as read :—OLDFIELD THOMAS, F.R.S., F.Z.S., "The Delacour Exploration of French Indo-China.—Mammals. II. On Mammals collected during the Winter of 1926-27"; S. MAULIK, F.Z.S., "New Chrysomelid Beetles from India, with a Note on the Scales of Coleptera."

The next Meeting of the Society for Scientific Business will be held on Tuesday, March 6th, 1928, at 5.30 P.M., when the following Communications will be made :—

H. HAROLD SCOTT, M.D., F.R.C.P., F.Z.S.

Report on the Deaths occurring in the Society's Gardens during the year 1927.

H. HAROLD SCOTT, M.D., F.R.C.P., F.Z.S.

Carcinoma of the Tonsil in a Common Wolf (*Canis lupus*).

Major M. CONNOLLY.

On a Collection of Land and Freshwater Mollusca from Southern Abyssinia.

ENID K. SIKES, B.Sc.

The External Morphology and Life-history of the Coccid Bug *Othezia urticæ* Linn.

The following Papers have been received :—

H. C. JAMES, B.Sc., Ph.D., N.D.A., N.D.D.

On the Post-Embryonic Development of the Female Genitalia and of other Structures in the Chalcidoid Insect *Harmolita graminicola* Gir.

DOROTHY J. JACKSON.

The Biology of *Dinocampus* (*Perilitus*) *rutilus* Ness, a Braconid Parasite of *Sitona lineata* Linn.

MARIE V. LEBOUR, D.Sc., F.Z.S.

The Larval Stages of the Plymouth Brachyura.

A Further Series of Reports on the Zoological Results of the Cambridge Expedition to the Suez Canal, 1924, by Prof. ARTURO PALOMBI, Dr. A. SCHELLENBERG, and F. A. POTTS, M.A.

G. C. ROBSON, M.A., F.Z.S.

On the Giant Octopus of New Zealand.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
February 28th, 1928.

No. 296.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

March 6th, 1928.

Prof. E. W. MacBride, F.R.S., Vice-President,
in the Chair.

The Secretary communicated a short "Note on Uganda Gorillas," by C. W. Chorley, F.Z.S.

Mr. F. Martin Duncan, F.Z.S., exhibited, and made remarks upon, a series of Cinematograph Films taken in the Society's Gardens.

Dr. H. H. Scott, F.R.C.P. Lond., F.Z.S., communicated his "Report on the Deaths occurring in the Society's Gardens during the Year 1927," and gave a *résumé* of his paper on "Carcinoma of the Tonsil in a Common Wolf (*Canis lupus*)."

Miss Enid K. Sikes, B.Sc., gave a *résumé* of her paper on "The External Morphology and Life-history of the Coccid Bug *Othezia urticæ* Linn."

In the absence of the Author, Major M. Connolly's paper, "On a Collection of Land and Freshwater Mollusca from Southern Abyssinia," was taken as read.

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

The next Meeting of the Society for Scientific Business will be held on Tuesday, March 20th, 1928, at **5.30** P.M., when the following Communications will be made :—

THE SECRETARY.

Report on the Additions to the Society's Menagerie during the month of February, 1928.

G. C. ROBSON, M.A., F.Z.S.

On the Giant Octopus of New Zealand.

H. HAROLD SCOTT, M.D., F.R.C.P., F.Z.S.

Tuberculosis in Marsupials.

H. C. JAMES, B.Sc., Ph.D., N.D.A., N.D.D.

On the Post-Embryonic Development of the Female Genitalia and of other Structures in the Chalcidoid Insect *Harmolita graminicola* Gir.

DOROTHY J. JACKSON.

The Biology of *Dinocampus* (*Perilitus*) *rutilus* Ness, a Braconid Parasite of *Sitona lineata* Linn.

MARIE V. LEBOUR, D.Sc., F.Z.S.

The Larval Stages of the Plymouth Brachyura.

The following Papers have been received :—

A Further Series of Reports on the Zoological Results of the Cambridge Expedition to the Suez Canal, 1924, by Prof. ARTURO PALOMBI, Dr. A. SCHELLENBERG, and F. A. POTTS, M.A.

ROBERT GURNEY. D.Sc., F.Z.S.

Some Copepoda from Tanganyika collected by Mr. S. R. B. Pask.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
March 13*th*, 1928.

No. 297.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.[*]

March 20th, 1928.

Major S. S. Flower, O.B.E., Vice-President,
in the Chair.

The Secretary read a Report on the Additions to the Society's Menagerie during the month of February, 1928.

The Secretary exhibited, and made remarks upon, a series of photographs of the Detroit Zoological Gardens.

Mr. G. C. Robson, M.A., F.Z.S., communicated his paper on "The Giant Octopus of New Zealand."

Dr. H. Harold Scott, F.R.C.P., F.Z.S., communicated his paper on "Tuberculosis in Marsupials."

In the absence of the Authors the following papers were taken as read:—H. C. James, B.Sc., Ph.D., "On the Post-Embryonic Development of the Female Genitalia and other Structures in the Chalcidoid Insect *Harmolita graminicola* Gir."; Dorothy J. Jackson, "The Biology of *Dinocampus* (*Perilitus*) *rutilus* Ness, a Braconid Parasite of *Sitona lineata* Linn."; Marie V. Lebour, D.Sc., F.Z.S., "The Larval Stages of the Plymouth Brachyura."

---

[*] This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

The next Meeting of the Society for Scientific Business will be held on Tuesday, April 3rd, 1928, at **5.30** P.M., when the following Communications will be made:—

Miss E. M. BROWN (Aquarium Research Fellow).

Exhibition of a Fluke (*Microcotyle alcedinis*) from the Gills of the Sea-Bream *Pagellus centrodontus*.

C. R. S. PITMAN.

(1) Notes on a young Pangolin captured in January 1928.
(2) Nkosi Island and its Sitatunga.

R. GURNEY, D.Sc., F.Z.S.

Some Copepoda from Tanganyika collected by Mr. S. R. B. Pask.

CAMBRIDGE SUEZ CANAL EXPEDITION REPORTS.

(1) Prof. ARTURO PALOMBI.

Report of Turbellaria.

(2) Dr. A. SCHELLENBERG.

Report on the Amphipoda.

(3) F. A. POTTS, M.A.

Report on the Sedentary Polychæts.

The following Papers have been received:—

J. H. LLOYD, M.Sc., F.Z.S.

Abnormalities of *Rana temporaria*, chiefly relating to the Vascular System.

J. G. MYERS, D.Sc.

Morphology of the Cicadidæ (Homoptera).

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
March 27th, 1928.

No. 298.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

April 3rd, 1928.

Prof. E. W. MacBride, F.R.S., Vice-President, in the Chair.

Miss E. M. Brown (Aquarium Research Fellow) exhibited, and made remarks upon, a Fluke (*Microcotyle* sp.) from the Gills of the Sea-Bream, *Pagellus centrodontus*.

Major S. S. Flower, O.B.E., F.Z.S., exhibited specimens of the great African Land-Tortoise (*Testudo sulcata*) to show:—(1) rate of growth and (2) tooth-like processes of the horny jaw.

Mr. F. Martin Duncan, F.Z.S., exhibited, and made remarks upon, specimens of Trapdoor-Spiders' nests from Queensland, and a female Huntsman-Spider (*Heterapoda venatorius*) with her egg-cocoon.

Mr. D. Seth-Smith, F.Z.S., exhibited, and made remarks upon, (1) a lead pipe gnawed by mice, and (2) photographs of the Society's New Bird House.

Mr. E. G. Boulenger, F.Z.S., exhibited, and made remarks upon, living specimens of the toad, *Pipa americana*.

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Mr. D. Seth-Smith, F.Z.S., communicated Mr. C. R. Pitman's (1) "Notes on a young Pangolin captured in January 1928" and (2) "Nkosi Island and its Sitatunga."

Mr. C. F. M. Swynnerton, C.M.Z.S., exhibited, and made remarks upon, photographs showing forest undergrowth cleared by the browsing of Sitatunga.

In the absence of the Authors, the following papers were taken as read:—R. Gurney, D.Sc., F.Z.S., "Some Copepoda from Tanganyika collected by Mr. S. R. B. Pask"; Cambridge Suez Canal Expedition Reports. (1) Prof. Arturo Palombi, "Report on the Turbellaria." (2) Dr. A. Schellenberg, "Report on the Amphipoda." F. A. Potts, M.A., "Report on the Sedentary Polychæts."

The next Meeting of the Society for Scientific Business will be held on Tuesday, April 17th, 1928, at **5.30** P.M., when the following Communications will be made:—

J. H. Lloyd, M.Sc., F.Z.S.

Abnormalities of *Rana temporaria*, chiefly relating to the Vascular System.

J. G. Myers, D.Sc.

Morphology of the Cicadidæ (Homoptera).

Harold G. Jackson, D.Sc., F.Z.S.

The Morphology of the Isopod Head.—Part II. The Terrestrial Isopods.

The following Papers have been received:—

J. H. Lloyd, M.Sc., F.Z.S., and Edith M. Sheppard, M.Sc., F.Z.S.

A Further Contribution to the Anatomy of a Hammerhead Shark (*Zygæna malleus* Shaw).

Hugh B. Cott, B.A., F.Z.S.

Report on the Zoological Society's Expedition to the Zambesi, 1927.

Cyril Crossland, M.A., F.Z.S.

Notes on the Ecology of the Reef-builders of Tahiti.

O. W. Richards, M.A.

The Species of *Notogonia* (Hymenoptera, *Larridæ*) occurring in the Mediterranean Basin.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary, Zool. Soc.

Zoological Society of London,
Regent's Park, London, N.W. 8.
April 10*th*, 1928.

No. 299.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

April 17th, 1928.

Prof. J. P. HILL, F.R.S., Vice-President,
in the Chair.

THE SECRETARY read a Report on the Additions to the Society's Menagerie during the month of March, 1928.

Mr. CLARENCE ELLIOTT exhibited, and made remarks upon, (1) specimens of Giant Barnacles from Chile, and (2) a living specimen of a Giant Tortoise (*Testudo microphyes*) from Albemarle Island (Galapagos Islands).

Lord ROTHSCHILD, D.Sc., F.R.S., F.Z.S., exhibited, and made remarks upon, photographs and skulls of various species of Giant Tortoises.

Dr. J. G. MYERS communicated his paper on the "Morphology of the Cicadidæ (Homoptera)."

Dr. HAROLD G. JACKSON, F.Z.S., gave a *résumé* of his paper on "The Morphology of the Isopod Head.—Part II. The Terrestrial Isopods."

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advanse.

In the absence of the Author, Mr. J. H. **Lloyd's** paper on "Abnormalities of *Rana temporaria*, chiefly relating to the Vascular System," was taken as read.

The next Meeting of the Society for Scientific Business will be held on Tuesday, May 1st, 1928, at **5.30** P.M., when the following Communications will be made:—

Dr. G. M. Vevers, F.Z.S., and Mr. R. A. Smith, B.A., V.P.S.A.

Exhibition of Flint Implements, Flakes, and Cores of Human Origin but of uncertain age collected at the Society's Estate at Whipsnade.

Hugh B. Cott, B.A., F.Z.S.

Report on the Zoological Soicety's Expedition to the Zambesi, 1927.

O. W. Richards, M.A.

The Species of *Notogonia* (Hymenoptera, *Larridæ*) occurring in the Mediterranean Basin.

James Waterston, B.D., D.Sc., F.Z.S.

The Mallophaga of Sand-Grouse.

The following Papers have been received:—

W. T. Calman, D.Sc., F.R.S., F.Z.S.

On the Prawns of the Family Atyidæ from Tanganyika.

Alexander Meek, D.Sc., F.Z.S.

On *Sagitta elegans* and *Sagitta setosa* from the Northumbrian Plankton.

Cyril Crossland, M.A., F.Z.S.

Notes on the Ecology of the Reef-builders of Tahiti.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great cost of paper and printing. Papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary, Zool. Soc.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8
April 24th, 1928.

I. A. R. I. 75.

IMPERIAL AGRICU[redacted]RESEARCH
INSTITUTE LIBRARY
NEW DELHI.

Date of issue.	Date of issue.	Date of issue.
12.2.44		
3 JUN 1955		
29.7		
21-7-64		
18 SEP 1967		